The Journal of HEREDITY

SANTA GERTRUDIS—A BREED ADAPTED TO SUBTROPICAL AREAS
(SEE PAGE 47)

EFFECTS OF CLIMATE ON ANIMAL PERFORMANCE—
A SPECIAL ISSUE

Effects of High Temperature
on Reproduction, Milk Production and Growth

Physiological Approaches to Animal Climatology

Breeding Considerations in Relation to Climatic Problems

Improving Livestock Environment in High Temperature Areas

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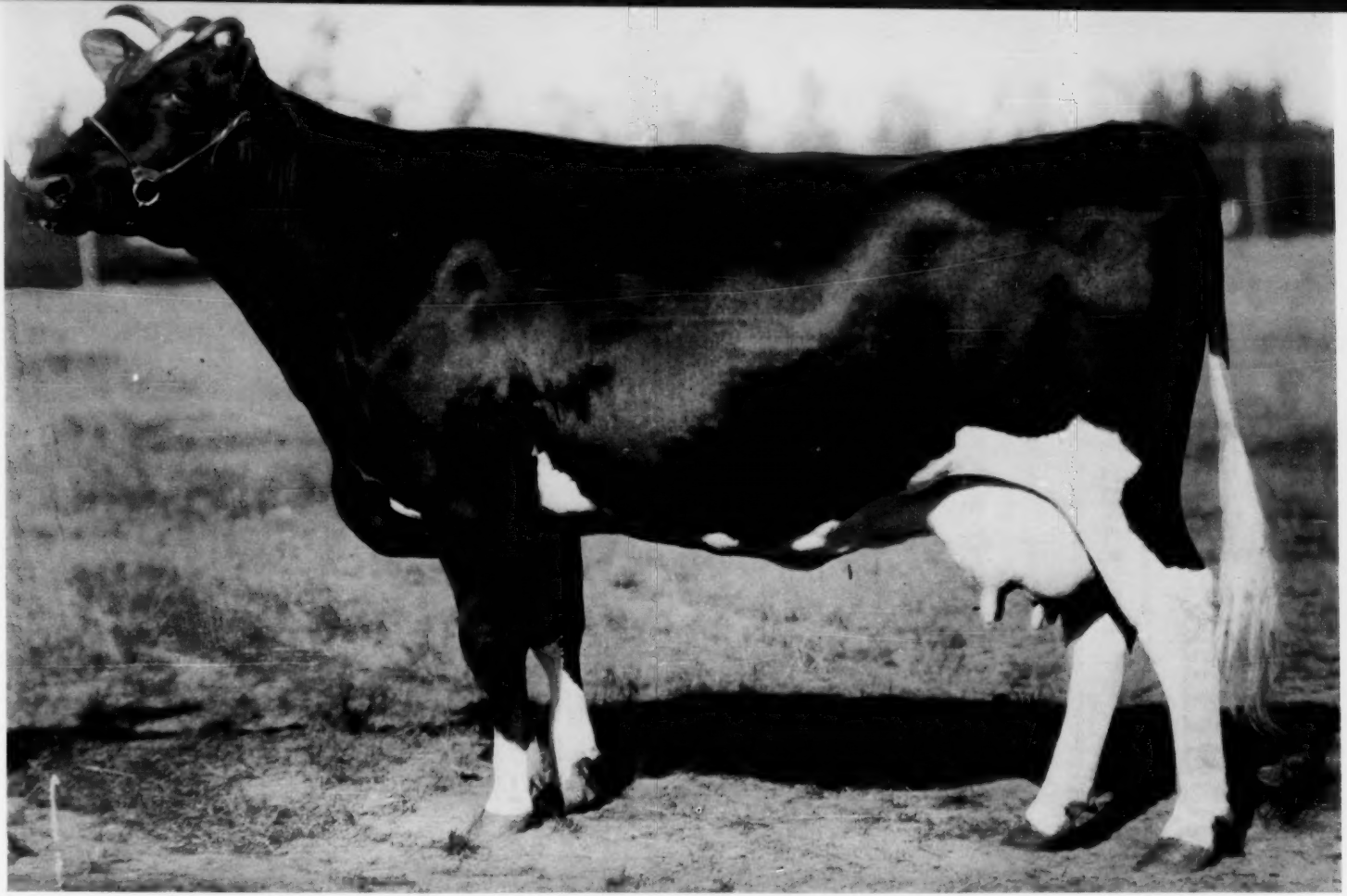


THE HOLSTEIN COW

Figure 1

The Holstein, developed on the lush pastures of the Netherlands, is highly specialized for milk production in areas of good feed supply, and now occupies an important place in most commercial dairy areas throughout the temperate zones.

THE EFFECTS OF CLIMATE ON ANIMALS AND THEIR PERFORMANCE

An Introduction to a Symposium

RALPH W. PHILLIPS*

ANIMAL geneticists, physiologists and livestock producers have been giving increasing attention, durthe the last 10 to 15 years, to the effects of climate on animals. Several factors have no doubt contributed to this trend.

Man, becoming generally more conscious of his nutritional requirements and of the need for more protein, in many regions if balanced diets are to be provided, has sought ways of producing that protein from animal sources. This is particularly true in the tropical and subtropical regions where human population pressures are heavy and where man obtains most of his food from plant sources.

Rapidly expanding human populations are contributing to keener competition between foods of animal and plant origin. The animal, in transforming plant materials into products usable by man, must use some of the original material for skeletal growth, for maintenance, etc. Thus, animal products are relatively expensive, and while they are generally highly valued because of their nutritional value as well as their taste, they must compete with less expensive foods from plant sources. In these circumstances, the animal geneticist must constantly seek ways of increasing the efficiency, or of "breaking through the performance barrier," in livestock.

Most of the research aimed at livestock improvement has been carried out in institutions located in the more productive regions of the temperate zones, using animals of types developed in and adapted to temperate climates (see Figure 1). These more productive regions have had the resources with which to develop research institutions, to train men, and to carry out livestock breeding research which is inherently expensive.

Livestock improvement has not received the same degree of attention in tropical and subtropical regions, high mountain areas, and semi-arid tracts although many useful types have been produced in such areas (see Figures 2, 3 and 4). Where work has been undertaken, the leaders have usually been trained in temperate-zone institutions and too often have tried to introduce temperate-zone animals and practices without due regard to the effects of climate.

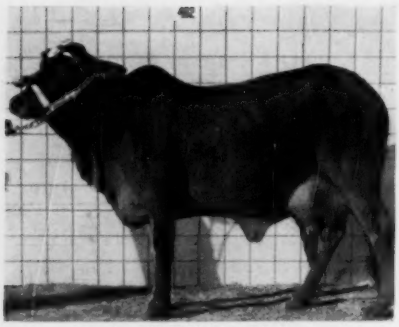
The years during and subsequent to World War II were certainly years when man moved about his globe more than at any time in history. Among those who moved about were experts in the field of animal production, genetics and physiology; and whether they travelled in connection with their specialties or on other assignments, many of those who travelled from well-developed temperate countries had good opportunities to see the problems of livestock production in relation to human needs and the environments in the less-developed areas. The things they have learned are gradually being put to use in their home countries and in the training of leaders from less-developed countries.

Young leaders, well aware of the problems of producing livestock in the less favorable environments, are appearing in increasing numbers around the globe.

Information is gradually becoming available to the public on the sources of breeding material that actually exist in the world and from which the animal geneticist may eventually draw in his attempts to develop types that will be

*Director of International Organization Affairs, Foreign Agricultural Service, U. S. Department of Agriculture, Washington 25, D. C.

occupies an important place in most commercial dairy areas throughout the temperate zones.



A SAHIWAL COW

Figure 2

The Sahiwal breed, native to Pakistan, is the highest milk-producer among the India-Pakistan zebus. Well adapted to hot climates, it has been used only to a limited extent outside Pakistan and India.

able to "break through the performance barrier" under various environmental conditions. Too, there is an increasing awareness that many of the less known types and breeds may be able to make important contributions in livestock improvement programs.

There is also an increasing awareness, within the United States, that there are a number of livestock-producing areas where we may be able to increase production and the efficiency of production by developing types of animals more adapted to the environment, or by attenuating the adverse effects of the environment, or both.

The Southern Agricultural Workers, at their meeting held in Little Rock, Arkansas, in February 1958, took account of this problem of animal climatology in the southeastern United States, by organizing a symposium on the effects of heat on animal performance. The symposium was a joint activity of the Animal Husbandry and Dairy Sections. The author of this introductory paper had the honor of serving as chairman.

Animal climatology problems had been recognized much earlier in the Gulf Coast area, both by pioneering practical breeders who introduced zebu cattle and who developed new types from zebu-European crossbred foundations, including the Santa Gertrudis (see Figure 6), as well as by a few animal breeding research workers who initiated work in this field. Climatological problems have also been recognized by livestock producers elsewhere (see Figure 7). But a general recognition of the problem leading to a scientific approach is more recent, and has been accompanied by the addition of animal geneticists and physiologists to the staffs of animal husbandry and dairy departments in many institutions and by the initiation of substantial research programs.

The symposium, although centering attention on the effects of heat, covered other environmental factors as well. The papers presented in that symposium are reproduced in this issue of the JOURNAL OF HEREDITY in order to make them generally available to geneticists and others interested in animal improvement. They include two papers dealing with the basic physiological reactions of animals to hot climates, two dealing with climatic effects upon milk production and growth and fattening, one dealing with efforts to modify the adverse effects of hot environments, and one summing up the application of present knowledge to livestock breeding programs.

These papers provide good evidence of the extent to which the physiologist, the geneticist, the engineer and the animal husbandman must cooperate in finding solutions to climatological problems. The paper presenting certain aspects of the engineering approach is the first of its type to appear in the JOURNAL OF HEREDITY. At first glance, it may appear outside the scope of the JOURNAL. But, it contains information that is important to the animal geneticist for two reasons: First, it demonstrates that in some cases the engineer may help the geneticist in the solution of a difficult environmental problem by tempering the adverse effects of the environment. Second, it underlines the importance of carefully standardizing and controlling environmental conditions if physiological and genetic studies, in relation to environmental effects, are to be most useful. Also, from the standpoint of the animal husband-

PINZGAU CATTLE
Figure 3
The Pinzgau, found in the Austrian-Bavarian Alps, is considered well adapted to Alpine grazing conditions.

man, it contains information of immediate practical value, and emphasizes the importance of management research. In the pursuit of knowledge of genetics, physiology and nutrition, the animal scientist has tended to overlook the need for research on the management aspects of livestock production.

In presenting papers from the Southern Agricultural Worker's symposium, mention should be made of a few other efforts aimed at stimulating work on problems of animal climatology, to indicate the nature and extent of the interest that is developing in this field.

On the international front, the Food and Agriculture Organization of the United Nations (FAO) has been active since the end of 1946 (see Figure 5). Problems of breeding in relation to the environment have occupied important places in discussions at regional meetings held in Lucknow, India and Turrialba, Costa Rica in 1950, Baurú, Brazil in 1952, Buenos Aires, Argentina and Brisbane, Australia in 1955[2,7,8,9,10]. Also, several monographic publications have been issued in the three officials languages of FAO (English, French and Spanish) to make the latest information generally available to workers around the world. These have included a publication on breeding livestock adapted to unfavorable environments (Phillips[6]); two describing the zebu cattle of India and Pakistan[3], the cattle of Africa[4] and the environmental conditions under which these cattle were developed; and one describing field tests of heat tolerance for use in livestock research[5].

In Europe, the increasing interest in environmental studies was reflected in a study meeting, organized by the European Association for Animal Production (E.A.A.P.) in Lucerne, Switzerland in 1954, on the influence of climate on animal production. The review papers and original contributions presented in that study meeting have been published by E.A.A.P.[1] Many of the papers quite naturally relate to problems encountered in high altitudes, and during cold winters which are encountered in many parts of Europe.

The papers to which brief reference is made above, and those cited in the six

LIVESTOCK FROM TWO CONTINENTS
Figure 4

Highland cattle of Scotland are shown in the upper photograph. These animals are used for beef production in the cool, damp hill country of Scotland. The lower photograph shows a Surti buffalo cow, one of several milking breeds found in India. In many tropical areas the water buffalo, rather than the cow, is the main milk producer.

symposium papers which follow, will indicate to the reader something of the scope of this subject of the effects of climate on animals and their performance. Readers will also find in these papers and references a great amount of detailed information. But to the discerning reader, it will soon become evident that there is much more to be learned than we now know. For here is a field of world-wide scope, and of great importance. Yet it is a field in which only small beginnings have been made: small beginnings at recording the facts about existing livestock types; small beginnings in unravelling the complex problems of physiological reactions to climatic factors; small beginnings in understanding the complex nature of the inheritance of the economically important traits in livestock, including the physiological bases of adaptability to the environment; and even smaller beginnings in applying the knowledge now available to livestock breeding and production.

The geneticists, the physiologists the

CONSULTANTS ON PLANT AND ANIMAL STOCKS
Figure 5

This group of scientists, which met in Washington, D. C. in May 1947, at the invitation of FAO, helped to plan an international program on genetic stocks of plants and animals. The participants (left to right) (seated) were P. V. Cardon, T. L. Bywater, S. J. Wellensiek, L. E. Kirk, Ralph W. Phillips, R. E. Buchanan, K .Loftus ills, (standing) M. J. Filippi, E. C. Elting, C. A. Krug, H. Scavenius, (not in picture) R. C. Cook, Robert F. Griggs, Walter Landauer, A. H. Moseman and S. H. Work

engineers, the animal husbandmen, and we must add the nutritionists, have an important field of joint endeavor and a field so large that the time for worry about "no new frontiers to conquer" is far distant.

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PHYSIOLOGICAL APPROACHES TO ANIMAL CLIMATOLOGY

R. E. McDowell*

In recent years a large amount of research has been conducted on the problem of heat in relation to the performance of livestock and poultry. This has been accomplished primarily through physiological studies of the responses of animals to various environments in the laboratory and field. These studies have been directed principally at: (a) developing tests which would indicate the relative tolerance of individuals or groups; (b) establishing the characteristics responsible for differences in heat tolerance; and (c) to an extent, the distribution of adaptability within existing breeds or groups.

Progress has been made, but at the present time the goal has been only partially achieved. Rather comprehensive reviews of literature on the environmental physiology of domestic animals have been published from time to time by Brody[10,11,12]; Findlay[19,22]; and by Lee and Phillips[35]. The general problem of animal adaptability to tropical and subtropical environments has also been reviewed in regional FAO conferences in recent years. This discussion will deal with some of the more recent findings on the effect of various climatic factors, principally in thermal environments, on the physiological reactions of cattle.

Body Temperature

There have been a large number of reports published on the relation of body temperature to environmental conditions in cattle. The normal body temperature for all breeds of cattle is usually accepted as 101°F.[10] with some deviation due to age, stage of lactation, level of nutrition[40] and reproductive state[48].

Most tests, which have been used to indicate heat tolerance, have used body temperature as a basis. The Iberia heat tolerance test, developed by Rhoad[42], was one of the first and most popular indices used. Attempts to further refine this test were made first by Gaalaas[24] and then Benezera[3]. The latter attempted to include respiration rate in addition to body temperature. Lee[34] also developed an index based on short time exposures in climatic chambers. These indices have proven helpful but have not been entirely satisfactory in assaying the effect of heat on animal performance.

Air temperature has a greater effect than any other climatic element on body temperature response[1, 9, 41, 45]. Studies under field conditions[6, 9, 24, 41, 48] have demonstrated that in European breeds, body temperature increases with increasing environmental temperature above 70° F.; with temperatures 80° F. and above showing a marked effect. Branton[9] found that at air temperatures of 78° to 94° F. the within cow correlation of rectal temperature and air temperature for lactating Holsteins and Jerseys was 0.77 and 0.67 respectively. Barrada[1] reports similar results with Holsteins. Quazi and Shrode[41] report that at air temperatures of 90° F. and above, the correlation of air temperature and rectal temperature in Holsteins, Jerseys and Jersey-Brahman crossbred cows was from 0.38 to 0.66, the lowest being in the crossbreds. Laboratory studies show similar results. Riek and Lee[43, 44] using seven hour exposures in a hot room, found that both Jersey cows and calves had abnormal temperatures at 85° F. Work at Missouri[52] has shown that rectal temperatures of Jersey, Brown Swiss and Holstein cows increased at air temperatures from 75 to 105° F. with Holsteins showing the greatest rise, while the rectal temperature of Brahman cows and heifers did not begin to rise until

*Dairy Husbandman, Animal Husbandry Research Division, Agricultural Research Service, U. S. Department of Agriculture.

the temperature exceeded 90° F. Studies with Zebu-European crosses[47] indicate that the degree of change in rectal temperature is inversely proportional to the amount of Sindhi blood.

In general, air temperatures above 80° F. influence the body temperature of cattle but the degree of effect is somewhat dependent upon breed, age, and stage of lactation and level of nutrition. The effect appears to be greatest in European breeds and to a lesser degree in Zebu crosses and Zebus. Calves (six months of age) appear to be more affected than adult animals[40, 44]; however, yearling heifers (12 to 22 months of age) appear to show about the same responses as that of adults[40, 47].

The conditions (hot-temperate-cold) under which animals exist between exposures to heat appear to influence rectal temperature responses. Repeatability coefficients for rectal temperature responses in studies at Beltsville[37] were fairly low until sorted into seasonal groups: April-July (low); August-September and February-March combined (high) and October-January (intermediate) for Jersey heifers eight to 22 months of age. The repeatability values were 0.93, 0.77 and 0.60 for the low, high and intermediate seasons, respectively. For dry cows, the value for Jerseys was 0.48 and that of Red Sindhi (F_1) crosses 0.42. This agrees closely with the work of Schein[47], with similar cattle in Louisiana and the values of 0.45 for Shorthorns and Herefords reported by Australian workers[16].

Several investigations have been made of the effect of humidity on the body temperature of cattle. Seath and Miller[46], Barrada[1] and Quazi and Shrode[41] suggest that under field conditions humidity has little or no effect on body temperature; whereas, Riek and Lee[45], Barrada[1] and Kibler[31] found a marked effect from studies in control chambers. The difference is probably due to differences in the environment under which the studies were made. At high air temperatures high humidity is no doubt an added factor in the distress of the animal.

Wind velocity appears to have a negative effect on body temperature changes. Work at Missouri[32] has shown that at air temperatures between 75 and 95° increasing air movement from 0.5 to five miles per hour reduced the rate of rise of rectal temperature.

The information on the effect of solar radiation intensity is not extensive at this point, nevertheless, from reports[1, 41, 49] it appears to be more important than wind velocity or humidity on temperature responses.

Respiratory Activity

An increase in respiration rate is one of the first visible responses cattle make to increasing air temperature. It is regarded as one of the primary mechanisms for the maintenance of heat balance in most animals. Numerous reports[1, 2, 3, 6, 24, 25, 26, 30, 34, 36, 40, 41, 43, 44, 47] have been published on the changes in activity with increasing air temperature. The results have demonstrated that rate increases with increasing air temperature and the change is most pronounced above 85° F. Barrada[1] reports that under chamber conditions vapor pressure has about the same effect on rate as air temperature but under field conditions vapor pressure had only a small effect. In the latter studies a 1° F. change in air temperature caused about five times as much change as 1 mmHg vapor pressure.

A high respiratory rate in most cases does not indicate the animal is successful in keeping its temperature balance but that it is already overheated and is trying to restore normal heat balance. Rate may increase only up to a point. Barrada[1] reports that at maximum stress (104° F. with 80 percent relative humidity) the rate reached its peak in the second hour (170/min for Jerseys and 150/min for Holsteins) after which it declined. This was considered the ceiling response or the limit of the physical capacity of the respiratory system. The decline following the peak was attributed to muscular fatigue, therefore, the muscles could not keep up the high rate continuously. This may well be one of the major causes of decline in respiratory rate after attaining its maximum physical capacity.

From field studies Beakly and Findlay[2], Louisiana workers[47] and others have concluded that the variability of respiratory rate with exposure time and environmental temperatures would make it of little value as an index of the ability to withstand thermal stress under field conditions. Studies in control chambers at Beltsville[37] have shown that repeatability coefficients for respiratory responses are low and remain low even after sorting by seasons. This agrees with the findings of Barrada[1]. Australian workers[16] on the other hand report

that under field conditions repeatability rates in Shorthorn and Herefords were of the magnitude of 0.8.

In the absence of other evidence lower respiratory rate under hot conditions, may indicate the animals with the lesser discomfort (Table I). Increased respiratory rate contributes to rapid cooling (losses may reach 1/5 to 1/3 of the total evaporative loss[1]) but this may be counteracted by increased heat production from the effort involved.

TABLE I. Comparative Reactions of Holsteins, Jerseys and Red Sindhi-Jersey F_1 Crosses to Hot Conditions*. (Adapted from lata by McDowell *et al.*[36] and Barrada[1])

Item	Holsteins	Jerseys	Crosses
Rectal Initial	100.5	101.4	101.8
Temp. Final	104.6	104.4	103.6
(°F) Diff.	4.1	3.1	1.9
Resp. Initial	86.2	88.4	73.9
Vol. Final	315.1	255.7	232.6
(l/min) Diff.	228.9	169.1	158.6
Resp. Initial	44.0	42.7	36.8
Rate Final	140.0	141.6	144.6
(/min) Diff.	96.0	98.9	107.9
Tidal Initial	3.50	2.11	2.07
Vol. Final	3.30	1.82	1.63
(l/resp) Diff.	0.20	0.29	0.45
Body wt. (lb)	1475	991	951
Age	5 yr. 1 mo.	4 yr. 7 mo.	3 yr. 10 mo.

*Three hours at 105° F. and 34 mm Hg vapor pressure.

While the rate is the aspect of respiratory activity which is most easily observed, it is the volume of air respired which determines the cooling effect. Reports of laboratory studies at Missouri[12], Louisiana[27] and Beltsville[36] indicate that rate and volume do not increase in the same proportion. High rates may develop a respiratory alkalosis with a decline in CO^2-combining power of the blood (Table II). Therefore, to compensate for one stress, other physiological processes may be upset which will produce even more drastic consequences. As shown by the data in Table II, cattle appear to have the ability to compensate for the alkalosis except under severe conditions (100° F. and humid) through the excretion of alkali by the kidneys. Under hot-dry conditions respiratory acidosis may occur but usually it is compensated.

Studies of respiratory volume changes in response to heat of Jerseys, Holsteins, and Red Sindhi crosses at Louisiana[27, 28] and at Beltsville[36] have indicated that on the average the crosses showed a greater reduction in tidal volume with increased rate (Table I). As a result, the crosses may have the ability to more efficiently utilize respiratory activity for evaporative cooling and thereby perhaps be less susceptible to respiratory alkalosis. The Jerseys and Holsteins, however, showed rather wide within breed variation in this respect.

Additional information is still needed in order to fully determine the effectiveness of respiratory activity under thermal stress and the individual variation in the efficiency of its use.

TABLE II. Changes in blood pH, plasma CO^2 content, CO^2 combining capacity, urine pH, and urine bicarbonate of dry Holstein cows subjected to various temperature and humidity regimes for six hour periods. (Adapted from Barrada[1])

Atmospheric conditions		Arterial blood	Plasma CO_2	Plasma CO_2 Combining	Urine	Urine
Temp.	Rel. Hum.	pH	Content	Capacity	pH	Bicarbonate
(°F)	(%)		(Vol. %)	(Vol. %)		(meq./l.)
77	80	0.11	1.1	0.2	—0.15	2.0
80	80	0.02	1.0	2.8	—0.34	—1.9
	20	—0.03	5.7	6.0	—0.12	—1.2
86	80	—0.04	0.2	—0.1	—0.13	1.2
	20	—0.05	3.6	4.9	0.16	0.9
90	80	0.05	0.8	—2.8	—0.04	1.2
	20	0.05	1.4	2.4	—0.02	1.6
95	80	—0.04	2.7	2.0	—0.04	0.9
	20	—0.04	2.2	2.6	0.03	4.8
100	80	0.18	—2.7	—3.2	0.21	5.5
	20	—0.06	3.9	3.8	0.03	0.4
104	80	0.33	—9.9	—5.4	0.71	3.9
	20	0.02	0.6	1.5	—0.08	2.0
108	20	—0.14	0.9	—0.3	—0.05	1.3
113	20	0.11	2.7	3.7	—0.02	3.7
130	20	0.13	—6.7	—10.0	0.23	8.7

Pulse Rate

At Missouri[30] air temperatures from 40 to 105° are reported to have caused a slight decrease in pulse rate of all animals but at 105° the rate increased in all animals except heifers. The increase in rate was associated with abnormal rectal temperatures of 106 and 108° F. Most reports appear to concur with these findings.

Physiological Characteristics Associated With Adaptability

From the results reported by Brody[12], Johnston[26], Rhoad[42], Robinson[45], Schein[46] and others on the responses of various groups of cattle, it is apparent that animals differ in their reactions to heat stress and in their overall tolerance to heat. It is considered that improvement in heat tolerance by breeding would be rendered more certain if attention were focused on those characteristics responsible for heat tolerance. Before this can be done it must be established what these characteristics are. The most striking contrasts in response to heat are between European and Zebu breeds. These groups differ to some extent in body form, therefore, it would be logical to suspect that the primary reason for the greater heat tolerance on the part of the Zebu may be due to differences in the ability to utilize various means of heat dissipation.

Surface Evaporation

For a long time it was not known whether or not cattle sweat. The presence of sweat glands has been investigated rather extensively by Findlay and co-workers[18, 20, 21] and Dowling[14] who have concluded that cattle possess sweat glands of the apocrine type at the base of each hair follicle over most of the body surface. Findlay and his group report that the glands in cattle have a poor blood supply and therefore a low moisture production. Ferguson and Dowling[17] report that Zebu cattle sweat more than the European breeds when exposed to high temperatures and humidities. They attribute this partially to differences in

TABLE III. Evaporative cooling and percentage of heat production that is dissipated by vaporization in European and Indian evolved cows at different ambient temperatures in comparison to man (Data from Brody[12])

Temp. °F	Evaporative cooling/individual/24 hr. European breeds*	Indian cows†	Man	Percentage of Heat Prod. vaporized European breeds	Indian cows	Man
	(Kg)	(Kg)	(Kg)	(%)	(%)	(%)
50	7.8	6.0	0.7	23	29	18
60	10.1	6.2	0.8	32	30	20
70	16.7	7.2	1.0	50	36	29
80	20.8	8.3	1.1	66	46	30
90	20.3	14.0	2.2	79	78	66
100	21.1	16.2	4.3	90	96	119
102	21.5	17.2	4.7	95	102	128
105	22.7	18.5	7.0	104	112	194

*Average of six Holsteins, eight Jerseys and three Brown Swiss lactating cows.
†Average of two lactating and three dry Brahmans.

TABLE IV. Evaporation (mg in 5 min from 10 sq. cm) from same cow in warm (81°F, 12 mm Hg) and hot (101°F, 30 mm Hg) rooms (Data from McDowell *et al.*[38])

Time from beginning exposure	Warm				Hot			
	Neck	Forechest	Paunch	Loin	Neck	Forechest	Paunch	Lion
2.08	7.0				29.7			
2.16		25.8				55.7		
2.24			15.4				36.2	
2.32				10.8				31.0
2.40	8.3				30.2			
2.48		20.1				51.9		
2.56			9.0				30.5	
3.04				4.8				27.2
3.12	5.2				28.2			
3.20		26.7				54.3		
3.28			13.2				24.9	
3.36				5.9				31.3

follicle population density. Results from the Missouri climatic laboratory[12] have shown that European cattle vaporize at a lower rate per unit of surface area than Zebu cattle, perhaps because the latter cattle produce less heat. They have reported that up to 80° F. Shorthorn heifers had a higher surface evaporation rate than Santa Gertrudis or Brahman heifers but the evaporation rate of the Brahman continued to rise with increasing air temperature; whereas, the Shorthorns showed little or no change above 80° F. From the same laboratory it has been reported that Holstein cows showed evaporation rates of up to 1.4 Kg or about three pounds per hour (Table III). Barrada[1] is also of the opinion that water is evaporated from the surface by Holsteins at a rate greatly in excess of that attributable to respiratory evaporation.

Results of studies at Beltsville (Table IV) indicate that rate of evaporation increases with increasing air temperature. Rate of output varies with different areas of the body surface and the output is maintained at a relatively uniform rate. From observations of 16 areas over the body, it was found that in general the area midway between the dorsal and ventral extremities of the body had the highest rate. The rate decreased to some extent as the dorsal and ventral surfaces were approached and the lowest rates were from the extremities which included the lower legs and head. Evaporation from the area of the dewlap was distinctly lower in the Sindhi-Jersey crosses than the corresponding area in the Jerseys (Table V). Under the conditions of study the evaporation rates from comparable areas of Jerseys and Sindi-Jersey F_1 crosses were not significantly different but the within group variation was large (Table V). Although moisture is seldom visible on the haircoat of cattle it is apparent that a large portion of the heat load may be dissipated through surface evaporation. Depth of coat, air movement and humidity no doubt determine to a large extent the rate and effectiveness of surface evaporation but as yet the relative effect of each has not been fully determined.

The age old question of whether or not the moisture available for evaporation comes from the sweat glands in cattle is still rather controversial, nevertheless, evidence is mounting from the histo-chemical techniques used by Australian workers[17] and iontophoresis techniques at Beltsville[39] which indicate that the major portion of the moisture is secreted by the sweat glands. The ability of cattle to sweat is by no means as well developed as in man (Table III) or in the horse but observations suggest that the rate of sweating in cattle varies to such an extent between individuals that its relation to heat tolerance should be investigated much further.

Surface Area

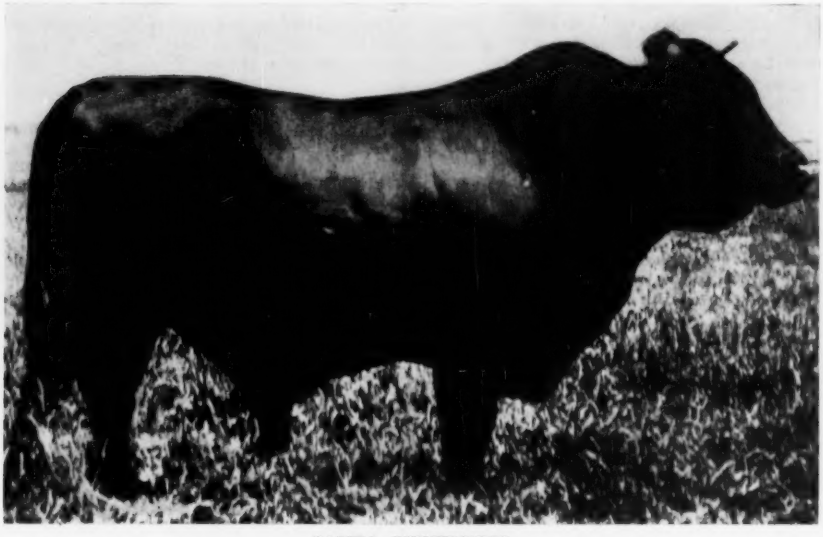
A large surface area should theoretically afford an advantage to an animal for dissipating heat by radiation and evaporation. Brody[12] states that Brahman cattle have 12 percent greater surface area and this is responsible in part for the greater heat tolerance of these cattle. On the other hand, studies conducted at Louisiana[27] and Beltsville with Holsteins, Jerseys and Sindhi crosses have shown that the greater heat tolerance on the part of the crosses was not primarily due to differences in proportional surface area even though the presence of large dewlaps, etc. might suggest that such a difference in area would be found. A larger surface area may be advantageous. However, it does not appear to be necessarily essential to good heat tolerance.

Coat Characteristics

In recent years attention has also been focused on the role of the coat of cattle in thermal stress. Bonsma[7, 8] has demonstrated superior growth, reproduction and production of smooth coated as compared to wooly-coated cattle and has shown that coat-type is heritable. Yeates[54] found, from studies in a psychometric chamber, that wooly-coated animals were at a disadvantage in the heat; a thick curly coat constituting a threat to the animals' life at 105°. Relief may be afforded by clipping long coats which was attributable to increased evaporation from the skin since evaporation is facilitated by short hair. Yeates concluded that the heat tolerance of an animal is closely associated with coat-type; those

TABLE V. Evaporation (mg. in 5 min. from 10 sq. cm) by Jersey and Sindhi-Jersey crossbred cows in a hot room (105°F, 34 mm Hg vapor pressure) (McDowell *et al.*[30])

	Jersey			Crossbreds		
	Forechest	Paunch	Ventral Neck Surface	Forechest	Paunch	Dewlap
	(mg.)	(mg.)	(mg.)	(mg.)	(mg.)	(mg.)
Mean	45.12	48.53	38.93	50.15	48.46	26.40
Standard Error	2.67	2.10	3.27	3.34	3.70	2.77
No. Animals	25	18	7	20	14	6



SANTA GERTRUDIS

Figure 6

The bull "Monkey", foundation sire of the Santa Gertrudis breed, based on a zebu Shorthorn foundation. This breed was developed to meet the requirements of beef production in the subtropical conditions of the Gulf Coast.

with short, flat, glossy coats proving superior. Also, he attributes the inability of some individuals of the European breeds to shed their wooly coat in the tropics to the light environment[55], the length of day in the tropics being insufficiently variable to operate the photoperiodic mechanism which controls the seasonal hair cycles of European breeds.

The Australian workers[16] report correlations of coat score with skin temperatures of 0.6 to 0.8, with rectal temperature 0.5 to 0.6 and with respiration rate 0.4 to 0.6. They are of the opinion that important differences are to be found in coat characteristics among animals in a relatively uniform herd of Hereford or Shorthorns, and these differences have considerable effect on heat regulation.

In the case of coat color, Bonsma[8] states that, other things being equal, a light color to reflect infra-red heat rays and a well-pigmented skin to absorb the ultraviolet wave lengths of sunlight should afford an advantage. There are also indications that air temperature may be a factor affecting coat color under hot conditions. Results at Missouri[12] have shown that increasing air temperatures from 65 to 95° F., even in the absence of solar radiation, caused the color of the hair of Swiss and Brahman cows to change to a lighter shade. The threshold for the color change appeared to be about 85° F. in the Brahman and 95° F. in Brown Swiss.

In general, cattle with a short smooth coat appear to have a superior tolerance over wooly-coated ones but the reason is not certain at this time. It is however, almost certainly related to some extent to surface evaporation.

Skin and Hair Temperature

Reports on the relation of skin and hair temperature[51, 53] have shown that increasing air temperature causes an increase in skin temperature but a large temperature gradient exists from the skin surface to the tip of the hairs. Brody and his colleagues[12] have shown that the gradient disappeared at temperatures of 100 to 105° F. They also found that Brahman cows had lower skin temperatures than European breeds up to about 105° F. but all groups were the same thereafter. From these studies skin temperature also appears to vary from region to region over the body surface. Australian workers[16] report a strong relationship between skin temperature and respiratory rate but a poor one with rectal temperature under field conditions.

Role of Appendages

The differences between Zebu and European breeds of cattle in thermoregulatory ability has been attributed in part to their large ears, dewlap, navel folds and prepuces. It has been demonstrated that the dewlap has a low surface

evaporation rate[39]. Studies on Red Sindhi bulls in the psychometric chamber at Beltsville before and after removal of the dewlap showed no appreciable differences in the rectal temperature or respiratory responses of these animals on either occasion (Table VI). The same was found to be true after removal of the hump and about four inches of each ear. A comparison of the number and size of blood vessels in the dewlap and the skin of the midneck region showed that the neck vessels were much larger and more numerous than in the dewlap area. Although insufficient as evidence by themselves, these results fit in with the growing belief that the dewlap and hump are not of great significance in heat regulation.

Blood Composition

Changes in blood constituents have been suggested as measures of adaptability. Reports by Blincoe and Brody[4] and Louisiana workers[46] indicate that high hemoglobin values are associated with high adaptability to extreme conditions of temperature. This is also true for specific gravity, the Ca : P ratio and the number of erythrocytes. High air temperatures appear to cause an increase in the circulating hemoglobin. Blincoe and Brody also report no obvious changes in blood composition until 65° F. and above when there is a marked increase in creatinine and a marked reduction in ascorbic acid and cholestrol levels. These changes were associated with reduced feed intake. Hematrocrit, erythrocyte and hemoglobin values were found to be higher in Brahman cows than European breeds. Studies by Ellmore[15] have shown that changes in eosinophils are not a satisfactory means of assaying heat tolerance because of the wide individual variation and low within animal correlation values.

Studies by Kunkel and co-workers[23, 33] with Holstein and Jersey cows during winter and summer showed significant breed differences for glutathione and gluthathione-hemoglobin ratio and significant seasonal differences with respect to glutathione, alkaline phosphatase and glutathione-hemoglobin ratios. Significant negative correlations were found between hemoglobin and current levels of milk production.

Thyroid Secretion Rate

Reports have shown there is a relationship between temperature and thyroid activity. Studies at Missouri[5] have shown that low temperatures (17° F.) increased thyroid activity of Jersey and Brahman cows 60 to 100 percent but showed no significant change in Holstein and Brown Swiss cattle. It is also reported that air temperatures of about 95° F. decreased the thyroid activity of all breeds by 30 to 65 percent. A daily temperature cycle of 10 to 40° F. increased thyroid activity by 20 percent over the values of a temperature cycle of 40 to 70° F. A temperature cycle of 70 to 100° F. decreased the activity about 30 percent below the 40 to 70° F. cycle. The authors state that these data roughly parallel heat production.

Studies conducted in Louisiana[29] have shown a 60 percent reduction in the estimated thyroid secretion rate (PBI levels) of lactating cows during the period from April to August.

From the present reports changes in blood constituents and thyroid activity appear promising as evidence in evaluating responses to thermal stress. It must be kept in mind, however, that changes in blood composition as well as thyroid activity are not due to heat alone but are also affected by feed intake. Much more work is needed in this field for if changes in blood constitutents and thyroid function can be related to factors controlling energy metabolism then they may prove helpful in assaying heat tolerance.

Heat Production

When the data on differences in ability to dissipate heat are assembled, they do not appear to explain adequately the observed dif-

TABLE VI. Reactions of Red Sindhi bulls to heat, before and after removal of the dewlap (McDowell, unpublished data)
(6 hours at 105°F and 34 mm Hg vapor pressure)

Test No.	Mean rectal temp. °F during exp.	Rise in rectal temp. °F over initial	Mean respiratory rate during exp.	Rise in respiratory rate over initial
		With dewlap		
1	101.87	1.27	120.3	84.3
2	102.18	1.58	141.7	105.7
3	102.08	1.28	136.7	100.7
Mean	102.04	1.38	132.9	96.9
		Without dewlap		
4	101.90	1.50	133.7	93.7
5	102.22	1.62	140.7	108.7
6	101.92	1.12	131.0	95.3
Mean	102.01	1.41	135.1	99.2

ferences in heat tolerance as judged by changes in rectal temperature, respiratory rate and physiological characteristics. The belief is fast growing that the important detriment to good performance under hot conditions lies not so much in the ability to lose heat but in greater efficiency in energy utilization thereby resulting in a lesser heat load.

Johnston[27] found from studies in Louisiana that the heat production of Sindhi-Holstein crossbred cattle was much less than that of Jerseys or Holsteins. The ratio of heat produced per square meter of surface area indicated that the crossbreds only had to lose 57 percent as much heat as the Holsteins and 76 percent as much as the Jerseys. The author concludes that the principle difference in the mechanism of thermo-equilibrium between the Red Sindhi crossbred cattle and the European breeds was in the heat production and the tendency for the crossbreds to maintain lower respiratory rates and rectal temperatures was due principally to the lower heat load. He attributed the lower heat load of the crosses to a lower basal metabolic rate since the heat increment per pound of FCM was the same for all three groups.

Missouri workers[12] report that they believe the high heat tolerance of Zebu cattle is partially attributable to their lower heat production. They report the critical temperature for decreases in heat production with increasing environmental temperatures as about 80° F. for Jersey and Holstein cows, about 85° F. for Brown Swiss cows, about 95° F. for Brown Swiss heifers and about 100° F. for Brahman cows (Table VII). Further, it appears that cows of European breeds tend to decrease heat production to a much greater extent than Zebu types when exposed to hot conditions (Table VII).

Because of the many factors which influence the heat production of an animal much more extensive studies are required in this field before results can be conclusive but in view of the present findings it appears that greater attention should be given this aspect of heat tolerance.

It may be seen from the foregoing that although the problems of adaptability in relation to tropical and subtropical conditions are far from settled, quite an array of physiological knowledge has been developed.

It appears that the ability of some animals to perform satisfactorily under hot conditions is due to: (1) differences in the capability of promoting heat loss; (2) differences in the efficiency of energy utilization; or (3) the ability to tolerate compensatory responses such as a rise in rectal temperature or respiratory activity. All animals possess some degree of adaptability but animals that continue to produce well under hot conditions could conceivably have both the capability of increasing heat loss and reduce heat production. It behooves the research worker, therefore, to investigate animal capabilities and determine whether or not within a given environment the most suitable animals possess all three to a high degree or if a compromise must be made.

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TABLE VII. Average heat production for different breed groups at various temperatures (Data from Brody[12])

Temp. °F	Jersey	Holstein	Br. Swiss	Brahman
	Heat Production cal/hr.			
60	646	794	723	512
65	686	800	742	
70	655	841	737	501
75	651	838	705	
80	614	830	675	447
85	597	773	674	424
90	500	629	584	434
95	477	609	598	398
100	396	568	577	418
105	402	554	544	414

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THE INFLUENCE OF HIGH TEMPERATURE ON REPRODUCTION

L. C. ULBERG*

IT is generally believed that high environmental temperatures are deleterious to both physiological and mental activities in the mammal. It is also known that reproduction is controlled by many physiological systems. Therefore, it would seem that high temperature could affect reproduction indirectly through such factors as the general well-being of the animal, feed intake, stress, or perhaps others. But high temperature could also act directly upon formation of sperm, ova and embryos or upon uterine environment in which embryos must develop. This report is not intended to be a complete, or a detailed literary review of the subject, but instead an attempt to bring together some of the data on the effect of high temperature upon the different reproductive processes.

At the beginning of the present century it was noted that a cryptorchid male produced no sperm and that it was possible to produce this condition experimentally by placing the testis in the abdominal cavity. These observations led to the idea that the higher temperatures of the abdominal cavity caused degeneration of the germinal epithelium[17]. Later it was shown that the testes were maintained at a lower temperature by a thermo-regulatory mechanism in the scrotum wall[18]. Semen quality could also be decreased by raising the temperature of the testes[15]. Since that time a large number of workers have studied this characteristic in males so that now it is generally agreed that high environmental temperature lowers semen quality in most species. This condition, particularly in rams during summer months, is usually referred to as "summer sterility."

Seasonal differences in spermatogenic activity and fertility in dairy bulls is also explained on the basis of higher summer environmental temperatures. For example, semen quality of bulls used in the stud at Louisiana State University decreased during the summer and early fall months and there was a decrease in the percent 60-90 day NRR of cows bred during this period[14]. Other workers from areas which are generally cooler during the summer months were not able to show this decrease in summer fertility[1, 10, 16]. Since estimated semen quality is used as a measure to predict the fertility of a particular sample of semen, keeping the males cool during periods of high environmental temperatures should maintain fertility.

Changing Environmental Temperatures

The next step in the study of the problem was an attempt to control semen quality by changing environmental temperatures. Again most of the reported data were obtained with rams kept cool during the summer. The percent fertilized ova from ewes mated to rams kept at 45-48° F. as compared to rams kept at prevailing summer temperatures was 64.2 and 26.0 respectively[8]. Rams kept at 65° F. produced semen of higher quality and settled more ewes than rams kept outside[9]. Generally an increase in environmental temperature above a certain point will cause an increase in body temperature and it is the increase in body temperature that apparently affects the fertility and sperm production of the rams or bulls. An increase in environmental temperature to 90°F. during the winter months increased rectal temperature and reduced semen quality in rams. Shearing rams during periods of exposure to high temperatures tended to prevent these changes. Under Wisconsin summer conditions sheared rams maintained high quality semen but fertility decreased. It was suggested that high temperatures caused a decrease in fertility before it caused a decrease in semen quality[13]. Casady, *et al.*[5], used temperature control chambers to show that temperatures of 85° F. for five weeks could injure spermatogenesis in the dairy bull. Also when a male was exposed to temperatures of 90-100°F. it required six to eight weeks for the rate of spermatogenesis to return to normal.

*Associate Professor of Animal Physiology, Animal Industry Department, North Carolina Experiment Station, Raleigh, N. C. Approved by the Director of Research for publication as Paper No. 909 in the Journal Series.

There exists the possibility that estimated semen quality as measured by sperm motility, abnormal sperm, etc. may not be a measure of fertility. There is another possibility: the female may not conceive as readily during periods of high environmental temperatures. A number of reports with data on laboratory animals show that high environmental temperatures or artificial fever will interfere with or destroy an early pregnancy[3, 4, 12]. Observations on sheep also indicate that high quality semen does not necessarily mean a high conception rate. For example, a 35 day non-return rate for ewes mated to rams with semen estimated to be of good quality was only 44 percent. This low non-return rate could be due to lowered female fertility caused by high environmental temperatures as well as lower fertility of semen estimated to be of high quality. The 35 day non-return rate could be increased during the summer months where ewes were kept at a temperature of 65° F. for 17 days post-mating. Cooling either the ewe or the ram resulted in a non-return rate of about 45 percent. When both the rams and the ewes were kept cool, the non-return rate was increased to 57 percent[9]. Yeates[21], mating ewes during the winter months, reported that a temperature of 105-110° F. for seven hours each day, starting one day after mating resulted in 12 conceptions from 20 matings. This is compared with 11 conceptions from 12 matings where the beginning of the heat treatment was delayed until 38 day post-matings. Eighteen conceptions resulted from 18 matings where no heat treatment was used. Ambient temperatures up to 99° F. had no apparent effect on sows pregnant for 85 or more days[11]. From these data it appears that the effect of high temperature upon the female in the production of young is prior to the time when much development of the embryo has occurred. If we are willing to accept this idea we are left with a number of theoretical possibilities to explain the results. Since sperm are susceptible to high temperature in the male tract they could be similarly affected in the female tract. The ovum or the young embryo could be affected either before or after fertilization. Also ability of the uterus to maintain an early pregnancy could be affected. Ewes placed in a room with temperatures of 90° F., just prior to the time of expected mating, had a decreased fertilization rate and an increased percent morphologically abnormal ova. Ewes placed in this environment eight days post-mating showed no effect from the increased temperature[6]. Under these conditions it would appear that either infertile ova are produced or that the damage is done prior to eight days post-mating.

Alliston and Ulberg[2] reported the results of an attempt to further study the problem by slaughtering ewes three to 14 days post-mating and observing the condition of the pregnancy. Twelve days post-estrus and during a month of high summer temperatures ewes were placed in a room kept at 65° F. Control ewes were kept in the shade but under normal atmospheric temperatures. Ewes from both groups were mated at the next estrus to rams with high quality semen. In the treated group 28 of 32 corpora lutea could be accounted for by what appeared to be normal developing embryos as compared with 12 normal embryos of 24 corpora lutea in the control group. There were no abnormal embryos detected after the shedding of the zona pellucida which occurs at about eight days post-mating. There may be, however, problems of technique in recovery of abnormal embryos more than eight days old. These observations are in accord with previously reported data from Kentucky except there was only one morphologically abnormal ovum recovered from the control group and none from the group in the cool room. A few ewes were kept at a constant temperature of about 93° F. and slaughtered six to 10 days post-mating. Here only one of eight ovulations resulted in normal embryos. The other ova showed signs of early degeneration. The embryos were recovered by flushing the oviduct, or uterus, with physiological saline solution. It was observed that some of the embryos would have distinct cell walls but would break down shortly after recovery. This would permit the yolk material to spread throughout the cavity within the zona and make it difficult to determine normal morphology. All such embryos were recovered from ewes which were not kept cool. One possible explanation for the breakdown of the cell walls is that the ova or embryos were already weak and added stress was caused by solutions used in flushing not being completely isotonic. In these studies high environmental temperatures seem to have an affect both upon formation of ova and upon very early development of the embryos. Information on this point in cows and heifers seems to be lacking. However, Ragsdale *et al.*[19] noted that two Holstein cows, bred for 4½ and six months, aborted two days after a 27-hour period of exposure to 100° F. temperature. So apparently high environmental temperatures can affect developing young embryos in a number of species.

A technique of reciprocal transplantation of six-day-old rabbit embryos was used by Shah[20] in an attempt to study this problem further. Forty-two embryos from does kept at an environmental temperature of 96°F. were transferred to does which were kept at normal room temperature. Thirty-five percent of these embryos developed into normal young. This is about the same result obtained from transfers where neither the host nor the donor was heat-treated. However, very few embryos from control does survived when placed in uteri of heat-treated does. He suggested that high environmental temperatures affect the embryos by

acting through the maternal tissues. Rats seem to be similarly affected.

Summary

High environmental temperatures can cause a decrease in fertility, semen quality and sperm production.

The production of young by females of many species is affected by high environmental temperatures. However, the specific reaction may depend upon the degree of temperature increase. The ova of females under constant high temperature may be affected directly prior to fertilization but less severe or variable temperatures may bring about a change in uterine environment so as to cause death of the embryo prior to the time of implantation.

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THE EFFECTS OF HIGH TEMPERATURES ON MILK PRODUCTION

JAMES E. JOHNSTON*

THE current interest in the effects of hot weather on milk production has developed as part of a broad, general recognition of the need for more efficient animal production in the subtropical and tropical regions of the world. Milk production of cattle in these areas has generally been much lower than in the temperate zone. Efforts have been made to improve this situation by importing high producing cattle from the temperate regions and also by crossing the temperate zone cattle with tropically adapted species. The results of these efforts have been variable but seldom have the milk production levels achieved compared favorably with those reported from the temperate areas. In the Gulf Coast region of the United States, where European breeds of dairy cattle are predominant, production records are generally lower than those of cattle with similar genetic background in the north. This difference has usually been attributed to the combined effect of poorer management practices and the long, hot summers of the South.

While there is still a need for more research we are now able to logically evaluate the factors affecting dairy production under hot conditions on the basis of research studies which have been conducted under field and climatic control chamber conditions. The control chamber work has provided us with a basic knowledge of the thermo-regulatory mechanisms of cattle[1,2,3,7,8,10,11,12]. The Missouri workers[1,2,10] have shown that the zone of thermal neutrality for lactating cattle lies between 30° and 60°F. depending on breed, production level and other metabolic factors. When environmental temperatures are reduced to as low as 0°F. there is little effect on milk production although a greater expenditure of energy for the maintenance of body temperature does occur. Thus, cattle are well adapted to cold conditions. When air temperature is raised above 60°F., however, cattle have more difficulty adapting and reduction in milk production has been reported to occur at temperatures of about 75°F. At high temperatures, humidity also becomes very important since more of the heat loss of the animal must occur through vaporization of water from the skin and respiratory tract. The air temperatures critical to milk production may thus vary considerably depending on the humidity.

Most of the climatic control chamber studies have been either of short duration (six to eight hours) or for long periods of time at constant temperature. While this type of work has been valuable in outlining basic mechanisms, the results cannot be readily interpreted in terms of animal response to natural climatic conditions due to the lack of diurnal variation. In natural climates there is usually a 20°F. or greater difference between daily maximum and minimum temperatures. In the Baton Rouge area, for example, summer afternoon temperatures will frequently exceed 95°F., while during the night they usually decline to 75°F. or less. These low night temperatures allow the animals to recover from heat stress experienced during the day and they are thus able to adjust to higher daytime temperatures than the control chamber studies might seem to indicate. Another factor which must be considered in field studies is the heat load due to solar radiation. Studies in Louisiana[6, 13] and California[5] indicate that these two factors have a marked effect on lactating cows. When adequate shade is provided, cows do very little grazing during the period from 8:00 a.m. to 4:00 p.m., but make up for this by increasing the time spent grazing at night. Holstein cows may do 75 percent or more of their grazing dur-

*Dairy Department, Louisiana Agricultural Experiment Station, Baton Rouge.

ing the hours of darkness. This makes it imperative that the best available pastures be reserved for night grazing if adequate forage intake is to be maintained. Many dairymen do not recognize these relationships and fail to provide necessary shade and adequate night pastures.

Level of Milk Production

The level of milk production has also been shown to influence the degree of response of cows to hot conditions. Field studies[5, 6] indicate that the highest producing cows tend to have the highest body temperatures and respiration rates on hot days. It has been estimated[2, 7] that each 1 lb. of fat-corrected milk (FCM) produced increases metabolic heat production by approximately 10 kilo calories of heat per hour. A 1000 lb. cow, with a resting heat production of 500 kilo calories per hour, producing 50 lb. of FCM per day would have a total metabolic heat load of 1000 kilo calories or double the resting heat load. Thus the higher the level of milk production the greater the heat stress on the cow. This effect has made the evaluation of the relative heat tolerance of lactating cattle difficult, particularly when wide ranges of production levels were involved as in the comparison of Indian and European breeds. The use of Red Sindhi-European crossbreds has made possible the study of the physiological mechanisms in cattle more productive than the pure Indian types. Results reported so far[7] indicate that these animals are more heat tolerant than animals of European breeding, at similar levels of production, but that this greater heat tolerance is probably due to a lower basal metabolic rate rather than to a higher efficiency of heat loss.

In addition to the studies in climatic control chambers, many field studies have been conducted[4, 5, 6, 9, 13, 14]. There has been a general tendency, in these studies, for milk production to fall and body temperature to rise with the onset of hot weather. As a result of this tendency for high body temperature and low production to be associated, a cause and effect relationship has frequently been assumed. The problem in making such an assumption is that hot weather affects both the animal and its feed supply. During the cool spring months in the South there are usually excellent pastures but as summer weather sets in there is a gradual decline in pasture quality. We, therefore, ask the question: "How much of the summer decline in milk production is due to the direct effect of hot weather on the cows and how much is due to change in forage quality and nutrient availability?" In an effort to evaluate these two variables the Louisiana State University climatic control chamber has been used to reduce the direct effect of hot weather on dairy cattle. The results of three such studies are summarized briefly in Table I.

During study 1 the air conditioning equipment was inadequate, providing only a 10° decrease in temperature which was accompanied by a rise in humidity. Groups A and C were fed chopped millet or grass silage during the day and grazed with Group P at night. The group differences in milk production were significant but the greatest difference was observed between the pasture and shade groups. The difference between these groups was primarily nutritional. Air conditioning during studies 2 and 3 was effective in completely eliminating heat stress. Groups A and C were fed freshly chopped forage day and night and managed the same except for temperature control. In study 2, air conditioning resulted in significantly more milk production during the

TABLE I. Effects of air conditioning on milk production, forage consumption and body temperature of lactating Holstein cows during summer weather

Study number	No. cows	Duration (days)	Maximum temperature (°F)	Maximum humidity (mm Hg.)	Fcm (lb/day)	Forage dry matter consumption (lb/day)	Afternoon body temperature (°F)
1 A*	10	120	82	21	30.5	—	102.7
1 C†	10	120	92	18	29.7	—	102.9
1 P‡	10	120	92	18	27.8	—	103.3
2 A	9	120	70	15	25.4	24.9	101.5
2 C	10	120	93	19	23.8	25.1	103.4
2 P	10	120	93	19	22.9	—	103.0
3 A	10	20	68	12	27.4	27.6	101.3
3 C	10	20	95	22	28.6	26.4	103.4

*Air conditioned.
†Shade barn
‡Pasture conditions

entire four-month period but the effect did not show up until 50 days after the study was started. Again, the pasture group produced less milk but the differences were not as great as in study 1, probably because pastures remained in better condition throughout the summer than in study 1. Study 3, conducted for a short period, showed no effect of air conditioning on milk production. In none of these studies was there any significant effect of hot weather on forage dry matter consumption. These studies, which have been conducted under natural hot conditions, indicate that within the range of climatic variations studied there is no immediate effect of hot weather on milk production as long as feed consumption is not affected. When cows which are not adapted to hot conditions are suddenly exposed to high temperatures, however, the first effect is a reduction in forage consumption which is followed by a reduction in milk production. Cows which are exposed to gradually increasing temperatures and humidities do not respond with an immediate reduction in milk production but show less persistency of production than cows protected from high temperatures. This effect does not show up until 30 days or more after initial exposure and is not necessarily associated with a marked reduction in feed consumption. The effect observed in adapted cows appears to be due to a reduction in metabolic rate which may be a result of lowered thyroid secretion rate. Current studies at Louisiana State University indicate that serum protein bound iodine levels of lactating cows fall 60 percent or more during the period from April to August and then rise very slowly during the fall and winter months.

Further evidence that high body temperatures and respiration rates do not, in themselves, cause a reduction in milk production is to be found in Table II. Note that the administration of thyroprotein resulted in an increase in both milk production and body temperature. This was associated with a rise in metabolic rate and a loss of body weight. These changes were most severe in the highest producing cows. The control group, on the other hand, reduced metabolic heat production and also milk production to some extent during the initial stages of adaptation.

During all of the studies cited above, milk production of both air conditioned and control groups of cows showed marked fluctuations as the result of changes in forage quality. Cows grazing summer permanent pasture have shown more marked reductions in production than have cows fed supplemental crops. It would appear that the most serious problem in the South is the maintenance of a supply of high quality forage through the summer. The use of supplemental crops such as millet and sudan may be helpful but these crops must be harvested at the proper stage of maturity if maximum production is to be maintained. In our trials, dry matter digestibility of millet dropped from 65 percent in the boot stage to 37 percent when the plants were allowed to head out prior to feeding.

The effect of hot conditions on milk composition has also been investigated. We have never been able to show a significant effect of hot weather on either butterfat percentage or solids-not-fat, although the mean butterfat percentage has always been lowest in the groups exposed to hot conditions. Increasing metabolism in the thyroprotein study, however, resulted in an increase in the butterfat percentage.

Summary

The effect of hot weather on dairy cattle may be either immediate or delayed depending on prior adaptation of the animals and severity of the heat stress. When lactating cows are suddenly exposed to hot conditions, to which they are not adapted, their immediate response is a depression of appetite which is followed by a reduction in milk production. When cows are allowed to adapt to hot weather gradually, as in the natural climate of the South, the reduction in milk production is delayed for a month or more and then occurs only gradually. This delayed response is probably associated with adaptive mechanisms, particularly the lowering of metabolic rate due to a depression of thyroid secretion rate. However, the principal cause of the "summer slump" in milk production is probably a decline in quantity and quality of forage available which

TABLE II. Effect of maintenance of metabolic rate through thyroprotein administration to Jersey cows exposed to hot conditions

			Group I				Group II*			
Period	Maximum temp. (°F)	Minimum temp. (°F)	Fcm (lb/day)	Body temp. (°F)	Metabolic heat (Cal/hr)	Body wt. (lb)	Fcm (lb/day)	Body temp. (°F)	Metabolic heat (Cal/hr)	Body wt. (lb)
1	70	55	15.94	101.6	—	775	15.94	101.5	—	797
2	95	75	15.64	104.2	581	730	17.40	105.4	797	724
3	95	75	14.26	103.5	—	719	16.06	105.3	—	681
4	95	75	14.32	103.7	589	727	14.93	105.3	883	673

*Group II fed 1½ grams thyroprotein per 100 lbs. of body weight periods 2 - 4.

may be aggravated by poor management practices. Hot weather, within the temperature ranges studied, does not have a marked effect on milk composition when digestible nutrient intake is maintained, although there appears to be a trend toward a slight lowering of fat percentage. This may also be associated with metabolic rate changes since artificial elevation of metabolism results in elevation of fat percentage. Adaptation of cows to hot weather carries over into the fall months and may account for difficulties encountered in achieving high levels of production during this period. Recent research indicates that high body temperatures alone do not necessarily result in lowered milk production. Lower milk production appears to occur only when appetites are reduced. More research needs to be done to determine whether animals showing the highest body temperatures may not be the most productive. This is a distinct possibility since high levels of milk production necessarily involve high metabolic heat production which makes the maintenance of normal body temperature difficult. There is also a pressing need for the development of better forage crops adapted to growth during hot weather.

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EFFECTS OF HIGH TEMPERATURES ON GROWTH AND FATTENING IN BEEF CATTLE, HOGS AND SHEEP

E. J. WARWICK*

ELEVATION of body temperatures and increases in respiration rate and heart beat to above "normal" levels following exposure to high environmental temperatures makes it probable that growth and fattening, in common with productivity of meat animals in other regards, would be adversely affected. Observation has long confirmed this expectation of deleterious effects upon growth rates and fattening. It is the purpose of this discussion to review the available evidence on the magnitude of such effects.

Swine

The extensive work of Heitman and associates at the University of California[6,7] under controlled conditions in a psychrometric chamber has done much to elucidate the effects of environmental temperatures upon gain and efficiency of feed utilization of swine. Table I, reproduced from their most recent publication, indicates that liveweight is significantly related to temperatures at which maximum gains are obtained. Pigs weighing from 100 to 150 pounds exhibited maximum gains at slightly over 70°F. Temperatures permitting maximum gains decreased gradually with increasing liveweight until at weights of approximately 350 pounds maximum gains were obtained at about 61°F. At 90°F. gains of less than one pound daily were observed at all live weights of 200 pounds or more. At 100°F. all weights over 100 pounds lost weight while those weighing 100 pounds gained only .39 pounds per day. At 110°F. even 100 pound pigs lost considerable weight. Efficiency of feed utilization measured in terms of feed per 100 pounds gain was closely related to environmental temperatures with the most efficient gains being made at the temperatures which permitted maximum gains. Efficiency declined very rapidly as the temperature moved away from the optimum. Heitman and Hughes[6] observed that evaporation of water was effective in reducing distress even at temperatures as high as 115°F.

Trials have been conducted in recent years by the U. S. Department of Agriculture on the question of whether the effects of certain hormone treatments vary at different environmental temperatures. Only the temperature effects will be considered here. The unpublished data of Johnston[14] shown in Table II, summarize the results of two experiments in which pigs were maintained at either 50° or 90°F. In one of these trials 150 pound pigs were kept on experiment for 32 days. Those maintained at 90°F. gained less than ⅛ pound per day and used nearly 1,000 pounds of feed per 100 pounds gain. In the other experiment, pigs were maintained at these temperatures from weaning to 200 pounds. The 90°F. temperature depressed gains by .35 pounds per day and feed per 100 pounds gain was slightly, although probably not significantly, increased. Table II also gives the results of other work reported earlier[15] in which a series of 28-day trials were conducted with pigs initially weighing 160 pounds or more. Gains were about .3 of a pound per day lower and the amount of feed required per 100 pounds gain was appreciably increased at 90°F. as compared to 50°F. Average backfat thickness at slaughter, used in these trials as a measure of carcass fatness, was very nearly the same at the two temperatures. If temperature had a differential effect upon lean and fat deposition it is doubtful that it would have been experienced to a measurable degree in trials of this short a duration. In another trial pigs initially weighing an average of 72 pounds were carried at temperatures of 80°F. and approximately 58°F. to live weights of approximately 200 pounds. In this trial considerable respiratory trouble was encountered at the lower temperature and gains were less than at 80°F. Perhaps this work might best be taken as an illustration of the fact that optimum temperatures do not necessarily guarantee good performance unless other factors are also satisfactory.

An experiment recently reported in abstract form[19] involved feeding pigs from an average weight of 150 pounds to 205 pounds at temperatures of 40°F. and 80°F. Pigs on experiment at 40°F. yielded a higher percentage of lean cuts and a lower percentage of fat trim than the 80°F. animals. These data are in line with observations of Pagé and Babineau[20] in which rats were reared for approximately 100 days at either room

*Acting Chief, Beef Cattle Research Branch, Agricultural Research Service, U. S. Department of Agriculture, Beltsville, Maryland.

temperature or in a cold room at 3°C. The rats raised in the cold room had significantly less total fat in their carcasses. The interpretation on this work was that the lower fat percentage in the rats raised in the cold room was a result of their greater physical activity which resulted in a greater proportion of the energy in their feed being used for physical activity and a lesser amount for the production and deposition of fat.

Practical hog men have long recognized that high temperatures were deleterious from the standpoint of performance in swine, and have attempted to make their animals more comfortable during extreme weather by providing shade or wallows. The observations of Jackson[13] at the Texas Station, in which pigs given access to a wallow gained 14 pounds more over a 90-day period than did control animals, and of Bray and Singletary[3], in which pigs in Louisiana having access to either a portable or a mud wallow gained approximately .4 pound per day faster than control pigs, are typical of results which have been observed with the use of such management practices.

Beef Cattle

It has long been recognized in a general way that beef cattle suffer at high environmental temperatures and that breeds differ in the degree to which this is the case. In summarizing work in this field the late Dr. Samuel Brody[4] stated that cattle of European breeds had a "comfort zone" from approximately 30 to 60°F. and that at about 80°F. their heat regulating mechanism began to fail with consequent distress and discomfort to the animal. In the case of Zebu cattle the "comfort zone" is approximately 50 to 80°F. and the heat-regulating mechanism does not begin to fail until temperatures of around 95°F. are reached.

The data presented in Table III of a trial recently completed at the Missouri station in cooperation with the U. S. Department of Agriculture in which cattle of different breeds were grown out over a considerable period of time at different controlled temperatures, is the only such experiment known to have been conducted[21]. As shown in the table, growth was depressed in Shorthorn cattle maintained at 80°F. as compared to similar animals maintained at a constant 50°F. temperature or in an open shed under climatic conditions at Columbia, Missouri. Gains of Santa Gertrudis heifers were apparently reduced, but to a lesser degree, by the increased temperature while Brahman heifers actually gained slightly more at 80°F. than at 50°F. over an 11-month period. These animals were not slaughtered at the conclusion of the trial so no data on carcass composition are available. However, photographs indicate that, as would be expected, those animals maintained at high temperatures and which failed to gain at normal rates definitely lacked finish.

An experiment conducted in New Zealand and on the island of Fiji[5] does not separate the effects of temperature from those of other climatic factors. The results, however, are of considerable interest. In this trial, eight pairs of monozygotic twin heifer calves of Jersey or Shorthorn breeding were divided with one member of each pair selected at random being raised in New Zealand and the other sent to Fiji. Feed from the same sources was fed at each location and the heifers were managed in a similar manner. At date of first calving the heifers raised on Fiji were 84 pounds or 9.6 percent lighter than their

TABLE II. Some effects of temperature on swine performance

	50° F.	90° F.
*150 lb. pigs, 32 day trial**		
Av. daily gain (lbs.)	1.17	.31
Feed/cwt. gain (lbs.)	495	974
*Weaning to 200 lb.**		
Av. daily gain (lbs.)	1.20	.85
Feed/cwt. gain (lbs.)	382	397
166 to 195 lb. pigs, Av. four 28-day trials†		
Av. daily gain (lbs.)	1.63	1.34
Feed/cwt. gain (lbs.)	404	457
Av. backfat thickness (mm)	40.4	39.7
	58° F	80° F
72 lb. pigs, 32-day trial†		
Av. daily gain (lbs.)	.77	1.23
Feed/cwt. gain	470	370

*Johnston, E. F. Unpublished data.
†Johnston, *et al.*[15]

TABLE I. Effect of ambient air temperature and mean liveweight on daily gain of swine*

Mean Liveweight (lb.)	Air Temperature							
	40°	50°	60°	70°	80°	90°	100°	110°
100		1.37	1.58	2.00	1.97	1.40	.39	—1.32
150	1.27	1.47	1.75	2.16	1.82	1.14	—.19	—2.60
200	1.19	1.57	1.91	2.22	1.67	.88	—.77	
250	1.10	1.67	2.08	2.14	1.51	.62	—1.36	
300	1.02	1.77	2.24	2.06	1.36	.36	—1.95	
350	.94	1.87	2.41	1.98	1.21	.10	—2.53	

*From Heitman *et al.*[7]

A HUT FOR HEAT PROTECTION

Figure 7

Animal climatological problems are often recognized under quite primitive conditions of livestock production. Here, in a Central Indian village, is the entrance to an underground hog-house, designed to protect the animals from the intense summer heat. (Photo by Ralph W. Phillips).

mates raised in New Zealand. Most of the difference in weight was due to the lower gain obtained during the hottest period of the year when mean temperatures exceeded 85°F. on Fiji.

The cooperative California-U. S. Department of Agriculture work under the extremely hot summer conditions at the Imperial Valley Field Station has been the most extensive to date on the problem of finding ways of improving the performance of beef cattle under extreme temperature conditions. Ittner and Kelly[10] found that shade increased the gains of beef cattle there and that gains improved appreciably after more effective shades were developed as compared with simple galvanized iron types, (Table IV). McDaniel and Roark[18] working in Louisiana found that shade, either artificial or natural, increased the gains of both cows and their suckling calves, (Table V). Pasture with abundant natural shade resulted in somewhat

TABLE III. Effect of temperature on growth of three breeds of heifers during periods of approximately three to 14 months of age*

	Environmental temperatures		
	50° F.	80° F.	Open shed
Av. weights, 3 mos. of age			
Santa Gertrudis	205	196	193
Brahman	194	199	140
Shorthorn	148	135	149
Av. weights, 14 mos. of age			
Santa Gertrudis	850	773	759
Brahman	700	739	675
Shorthorn	736	544	669
Weight increase 3-14 mos.			
Santa Gertrudis	645	577	566
Brahman	506	540	535
Shorthorn	588	409	520

*Ragsdale, *et al.*[21]

better gains than either artificial shade or scanty natural shade.

Shades do not necessarily increase cattle gains under southern conditions. This is brought out by the results shown in Table VI of an experiment conducted by McCormick *et al.*[17]. In this experiment a comparison of no shade versus either straw shades or aluminum shades resulted in lower average daily gain for both types of shades over a 4-month period (May 16 to September 18, 1957) than were obtained in pastures without shade. Gains were not appreciably affected by shade when cattle were full fed either on pasture or in dry lot during the period August 14 to November 6, 1957. Temperatures were much less extreme at Tifton, Georgia during this period than those normally encountered in the Imperial Valley of California.

The California work[1], extending over a period of years, has indicated that any means of reducing the environmental temperature is likely to be effective in improving cattle performance under their conditions. In one trial (Table VII) Hereford calves receiving cooled drinking water gained an average of approximately .4 of a pound more per day than those with uncooled drinking water which averaged about 88° in temperature. A few Brahman calves fed in the same trial with uncooled drinking water gained about as fast as Herefords receiving the cooled water. Further experimentation along this line indicated that the use of cooled drinking water was effective in making steers more comfortable and in increasing gains either on rations of hay or upon fattening rations including both grain and hay. Comparisons of cattle gains in wire corrals with those in wood corrals where air circulation was appreciably less, indicated greater gains in the wire corrals. (Table VIII). In addition to the corral differences the wire corral had a shallow water tank in which evaporation produced somewhat cooler drinking water than was supplied to animals in the other corral. Two years' work with fans as a means of promoting air circulation has also been effective in improving cattle gains.

Sheep

Apparently no specific experiments have been conducted to study growth and productivity of sheep under conditions of varying environmental temperatures. Fundamental laboratory work (see Lee and Phillips[16] for references) has shown, however, that while breeds of sheep apparently differ considerably in their heat-regulating ability, animals of most breeds develop higher than normal body

TABLE V. Effects of shade on summer gains of Hereford and Angus cows and calves in Louisiana, 1951-54*

	Av. daily gains (lbs.)	
	Cows	Suckling calves
No shade	—.05	1.18
Artificial shade	.84	1.78
Scanty natural shade	1.00	1.64
Abundant natural shade	1.29	1.85

*McDaniel and Roark[18].

TABLE VI. Effects of artificial shades on steer gains at Tifton, Ga., 1957*

	Straw shade	Aluminum shade	No shade
Coastal Bermuda Pasture			
May 16 - Sept. 18			
No. steers	9	9	9
Av. daily gain (lbs.)	1.28	1.26	1.45
Fattening rations on pasture			
Aug. 14 - Nov. 6			
No. steers		8	8
Av. daily gain (lbs.)		2.18	2.09
Fattening rations in drylot			
Aug. 14 - Nov. 6			
No. steers		8	8
Av. daily gain (lbs.)		2.58	2.60

*McCormick *et al.*[17]

TABLE IV. Effects of shades of various types and an evaporative desert cooler on atmospheric and ground temperatures and steer gains*

	Galvanized iron shade	Hay and galvanized iron shade and sprinkler	Aluminum and burlap shade and sprinkler	Desert cooler
Air temp. 8/6/48 (outside temp. 103.3° F.)	104° F.	101.5° F.	101.5° F.	96.5° F.
Ground temp. in shadow	107.5° F.	100° F.	97.2° F.	95.3° F.
No. steers	5	5	6	5
Av. daily gain (lbs.) (7/28/48 to 9/20/48)	.69	.89	.80	1.05

*Ittner and Kelly[10].

temperature in environments of 80 to 90°F. or above. Presumably this would be reflected in lower gains and a decreased rate of fattening.

One study has been carried out with sheep under differing environmental conditions, where temperature as well as other factors varied, so it was not possible to isolate the specific effects of higher temperatures[22]. The work was carried out in the high, cool range country at and near Dubois, Idaho and under warmer climatic conditions at Quincy, Florida. Carefully paired groups of Columbia sheep were selected at Dubois, Idaho, and one of each pair of ewes or rams was retained at Dubois and the other sent to Quincy. Studies of their performance and the performance of their offspring indicated that wool production was pratically equal at the two places but that the ewes at Dubois reproduced at a higher rate (1.15 lambs per ewe compared with .77 at Quincy), and that their lambs weighed about 15 pounds more per head at weaning time.

From a practical standpoint, work by Bosman[2], in South Africa indicated that when ewes and their lambs grazing on alfalfa pasture were allowed shade, the weights of the lambs were approximately six pounds greater after 87 days than were the lambs where neither the ewes nor the lambs were allowed shade. The former reached slaughter weight at 114 days and the latter at 135 days.

Discussion and Summary

From both practical and technical standpoints, it is apparent that much is still unknown in this general field. For instance, it is uncertain whether environmental temperatures have effects on relative rates of growth and deposition of fat and lean, independent of their effects on gain and independent of feed consumption. It is not known what length

TABLE VII. Effects of cooled drinking water on gains of Hereford steers in California*

	Cooled water (Av. 66° F.)	Uncooled water (Av. 89° F.)
1950 trial (alfalfa ration)		
Av. max. temp. 100.5° F.		
Av. min. temp. 70.2° F.		
Mean temp. 85.4° F.		
No. steers (Herefords)	11	11
Av. initial wt. (lbs.)	849	833
Av. daily gain (lbs.)	1.46	1.07
Av. daily water cons. (gallons)	15.4	16.6
Av. daily feed cons. (lbs.)	23.6	22.4
Feed/cwt. gain (lbs.)	1618	2092
1953 trial (alfalfa and oat hay ration)		
Av. daily gain (lbs.)	1.04	.78
1953 trial (hay and grain ration)		
Av. daily gain (lbs.)	1.51	1.18
1952 trial (alfalfa ration)		
Av. daily gain (lbs.)	2.01	1.57

*Ittner *et al.*[12] and Ittner *et al.*[8].

TABLE VIII. Effects of type of corral fence and of fans on steer gains in California

	No. steers	Av. initial wt. (lbs.)	Av. daily gain (lbs.)	Av. feed/cwt. gain (lbs.)
*Type of fence and water tank**				
Wood fence, deep water tank	7	815	1.51	1157
Wire fence, shallow water tank	7	815	1.94	923
Fans†‡*				
Fan	14	667	2.36	866
No Fan	12	663	1.56	1156

*Ittner *et al.*[9].
†Ittner *et al.*[11].
‡Av. max. temp. 102.8° F.
Av. min. temp. 76.2° F.
Mean temp. 89.3° F.

of exposure to high temperatures an animal can withstand (i. e. how many hours per day) without adverse effects on gain; nor do we know whether a single exposure to a high temperature has a long-lived or a short-lived effect. Among unanswered questions of a fundamental nature but with definite practical implications might be mentioned the following: Is gain affected by temperature other than through a depressing effect of high temperature on feed consumption? How do high environmental temperatures affect rumen microorganisms? If they change the microflora, how much exposure to high temperatures is required and how long is the recovery period with moderate temperatures?

In summary, it is apparent that high environmental temperatures reduce growth rate and presumably result in lower rates of fattening in cattle and hogs, and probably in sheep. Apparently any method of reducing the temperature and making the animals more comfortable is likely to be reflected in higher performance. Only one trial is known to have been reported in farm animals in which temperature affected fattening independent of rate of gain.

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IMPROVING LIVESTOCK ENVIRONMENT IN HIGH TEMPERATURE AREAS

T. E. Bond, C. F. Kelly and Hubert Heitman, Jr.*

ENGINEERS may enjoy somewhat of an advantage over the animal physiologist in relation to hot-weather animal comfort. There is a rather natural division of interest and responsibility with the physiologist considering *heat production and methods of reducing it*, and the engineer considering *heat loss and methods of increasing it*. Engineers can work with established laws of heat transfer that are more tangible than most animal physiological functions with which physiologists must work.

Considering only the exterior transfer of animal heat, the problem can be reduced to an idealized three-component system concerning the transfer of heat between an *animal*, its *surroundings*, and the *climatic environment*. With such a system the engineer is in a position to rationalize the influence of housing and facilities on the external loss of heat from an animal.

Laws governing the four methods of heat transfer[12, 13, 14] indicate quite explicitly the factors that can be altered to change the rate of heat transferred in this idealized system. Bionomical systems are seldom ideal so any rationalization regarding hot-weather animal comfort may be upset because of the influence of the somewhat intangible animal physiological functions, the interdependence of the heat transfer equations and, of course, the economic principles that limit alterations. Nevertheless, such idealization does provide a basic approach to guide the engineer toward the objective of improving summer housing for livestock.

This paper presents the four fundamental equations governing the transfer of heat by radiation, convection, evaporation and conduction, and describes their use in a basic approach to the problem of improving livestock environment in high temperature areas. The principles were applied in studies with beef cattle and swine, conducted cooperatively by the U. S. Department of Agriculture and the California Agricultural Experiment Station, at Davis and at the University of California's Imperial Valley Field Station at El Centro. The results indicate several ways in which the environment may be improved and also have an important bearing on the problems of standardizing or otherwise controlling the conditions under which genetic studies with livestock may be carried out.

Radiation

The radiant heat transfer can be described by the equation:

$$q_r = A\ F_s F_e\ \sigma\ (T_{ss}^4 - T_s^4)$$

where: q_r = rate of radiant heat transfer, Btu/hr.

T_s, T_{ss} = absolute temperature (t + 460) of surroundings and animal surface, °F.

A = area of a radiating object, sq. ft.

σ = Stefan-Boltzman constant, 0.174×10^{-8}

$F_s F_e$ = shape factor and emissivity factor

This equation shows that the amount of radiant heat transferred can be changed by altering the temperature of the surroundings (t_s), the temperature of the animal surface (t_{ss}), the shape factor (F_s), the emissivity factor (F_e), or the area of one of the radiating objects.

The surroundings of an animal include the sun, sky, shade, fences, buildings—any object or surface that might exchange heat with an animal. Lowering the temperature of the surroundings will reduce the radiation load on an animal, or increase its radiation loss. This cannot always be done economically. It is generally easier to protect animals from the hottest surroundings and to increase their exposure to cool objects and surfaces.

*Agricultural Engineer, AERD, U. S. Department of Agriculture; Professor of Agricultural Engineering; and Associate Professor of Animal Husbandry, University of California, Davis, California, respectively. The authors wish to express their great appreciation for the guidance of N. R. Ittner (deceased), without whose leadership, inspiration, imagination, and industry the studies at the Imperial Valley Field Station would not have been possible.

By shading an animal from the sun the radiant heat load on it can be reduced from 30 to 50 percent[9]. Spherical radiometers and black globe thermometers[1] have been used to measure the differences in radiant heat loads on shaded and unshaded animals. For example, on a typical August day in the Imperial Valley of California, the radiant heat load may be reduced from 244 to 167 Btu/hr ft^2 of animal surface by shade alone[2]. This is equivalent to reducing the mean radiant temperature* from 153 to 98°F. and means that a net radiant gain to the animal of about 70 Btu/hr ft^2 could actually be reduced to a net loss by shading.

One of the coolest areas of the surroundings is sky, and because of this an animal should have maximum exposure to it. From a series of radiometer observations in the Imperial Valley, Kelly *et al.*[10] found a linear relationship between air temperature and the temperature of a cloud-free sky such that the sky was about 28°F. cooler than the air when air was 100°F., and about 22°F. cooler when the air temperature was 110°F. This suggests that when the air temperature is 100°F. an animal should lose 20 to 25 Btu/hr ft^2 from its surface exposed to a clear sky (when sun is excluded).

Although shades protect animals from the sun, the temperature of most shade materials exposed to the sun will be higher than that of an animal's surface and will, therefore, be an additional surface that should be cooled. In a 54-day feeding trial in the Imperial Valley[6], Hereford steers gained an additional 0.20 pounds daily, and consumed 139 lb. less feed per 100 pounds gain, because their shade was artificially cooled. Their hay-covered shade had a sprinkled galvanized sub-roof that was at times 36°F. cooler than a galvanized steel shade in the control pen.

Artificial cooling of surrounding surfaces, such as shades, can be expensive. Proper choice of materials can be helpful. Tests were made of 35 different materials that might be used on animal shades, including different surface treatments of several of the materials. By comparing these to a common material, aluminum, an effectiveness scale was established as a ratio of the reduction in radiant heat load under a sample shade to the reduction under the aluminum shade. These materials ranged from hay, at the top of the effectiveness scale, down through galvanized steel, louvered shades, plywood, and several types of plastics —some with various color treatments—to snow fencing at the bottom of the scale. Ironically, the best and worst materials tested, hay and snow fencing, respectively, happen to be the two most used for animal shades in the Imperial Valley. On an average summer day there would be a difference in radiant heat load under shades made of these two materials of about 60 Btu/hr ft^2 of animal surface. This study showed also that the under surface of shade materials should have radiation characteristics similar to black surfaces to reduce the reflection of secondary radiation from the hot ground and surrounding objects to animals. White paint on the upper or outer surface is effective in reducing the temperature of many shade and building materials. Bond *et al.*[3] determined air temperature differences of 28°F. inside white painted and unpainted steel buildings when outside air temperature was 102°F.

It is important that ground and surrounding objects such as fences and buildings be as cool as possible. In Imperial Valley tests[7] Hereford steers in a wire pen located in an alfalfa field gained 0.43 lb. more daily during an 84-day feeding trial than a control group in a wood-fence pen. A comparison of environmental conditions in the pens indicated differences of about 4°F. in air temperature and about 10 Btu/hr ft^2 in radiant heat load, both to the advantage of the wire pen. Part of the increased gain may have been due to increased convection loss. This will be discussed later.

The shape factor (F_s) identifies the percent of exposure of the animal surface to surrounding objects. It should be large for radiation sources cooler than an animal's surface—sources like the sky. A shade reduces the shape factor of the sun to zero, which is fine, but it also reduces the shape factor of the cool sky with respect to an animal. A louvered shade is one method of improving this situation. A very small shade high in the air would be ideally good because the shape factor would be zero for the sun, small for the shade, and large for the sky. There are practical limitations to this but shades should be high. In actual choice tests[6] beef cattle used a 12-foot-high shade almost exclusively in preference to a 7-foot shade of equal size and accessibility. A long narrow shade oriented east and west will provide animals with greater exposure to cool north sky and shaded ground. The shape factor of hot, or highly reflective, buildings and objects can be lowered by increasing the distance between them and the animals.

The emissivity factor (F_e) combines the surface radiation characteristics so that both objects should have a low emissivity† when the animal is the coolest object, and both should have a high emissivity when the animal is the hottest. This suggests that the ground, the

*Mean radiant temperature of an environment is the temperature of a uniform black enclosure with which an object would exchange the same amount of energy as in the actual environment.

†Emissivity: the ratio of the intensity of radiation of any given wave length emitted from unit area of a surface to the intensity in the same wave length from unit area of a black body at the same temperature.

underside of the shade, and all hot surrounding objects should have a low emissivity. This is not completely true—it was found[2] that the underside of a shade should actually have a high emissivity. This is because of secondary, or reflected, radiation from sources outside the system being considered. An evaluation of surface radiation characteristics must be handled with caution.

Convection

The rate of convection heat exchange can be described by the equation:

$$q_c = CA_cV^n\ (t_{as} - t_{air})$$

Convection heat transfer is a function of the temperature difference between an animal's surface and air ($t_{as} - t_{air}$), air velocity (V), the effective convection surface (A_c), and a convection coefficient (C). While the convection coefficient is undoubtedly a function of the surface characteristics and shape of an animal, it is an experimentally determined quantity which, like the velocity exponential (n), has not been determined for livestock. However, for the present consideration, the form of the relationship is important rather than the magnitudes.

The surface temperature of animals varies with air temperature but at a slower rate. At low air temperatures an animal's surface temperature may be considerably greater so that there is a high potential for convective cooling. This potential diminishes as air temperature increases so that as some temperatures around or above 103°F., for most animals, the potential reverses and the animal is then subject to convective heating. For example, from calorimeter studies with swine[4] it was found that the percent of heat they lose by convection is reduced from 38 to five percent as air temperature increases from 40 to 100°F. When temperatures are high and cooling needs are greatest the convection potential is low. According to the above equation this potential can be increased by increasing the air velocity. Using fans to increase the average flow over Hereford steers from 0.6 to 3.7 mph during two separate 70-day feeding periods resulted in additional daily gains of 1.03 and 0.53 pounds per animal in Imperial Valley tests[8]. Heavy wood fences reduce air flow. In the comparison of wood-fence and wire-fence pens previously mentioned[7] the average wind velocity was 1.32 mph greater in the wire pen. Part of the increased daily gain of 0.43 lb. was attributed to a cooler environment, and part to the additional wind in the wire pen. The two effects could not be separated.

Evaporation

The transfer of heat by evaporation can be described by the equation:

$$q_e = K\ A_e\ V^n\ (P_s - P_a)$$

Evaporation heat loss can be increased by increasing the air velocity (V), by increasing the vapor pressure of water (P_a) at the animal's skin surface, by reducing the vapor pressure of water in the air (P_a), or by increasing the wet area (A_e) of the animal. Neither the evaporative constant (K) nor the velocity exponential (n) has been experimentally determined for livestock.

Evaporative and convective effects are not always easy to separate. In the beef cattle wind tests previously referred to[8], part of the benefit from increased air flow was probably due to increased evaporation. During 30 of the 70 test days the air temperature was above 103°F. and there probably was little or no benefit from convective cooling during these periods. At a time when the air temperature was about 100°F. an increase in air movement from 20 to 400 fpm reduced the body temperature of Hereford steers 1.15°F. and reduced their skin temperatures 2.6°F. In calorimeter tests with swine an increase in air velocity from 35 to 300 fpm caused surface temperature reduction of 13°F. with 50°F. air temperature, 7.4°F. when air temperature was 70°, and a 2.6°F. reduction at 90°F. In these same calorimeter tests the combined evaporative-convective heat loss increased 50 percent at the higher air velocity at 90°F.—it more than doubled at 70°F. The total heat loss increased correspondingly.

There is undoubtedly a limit to the amount that air velocity can be increased to increase evaporation, at least without supplying additional surface water to the animal. The vapor pressure of water at the skin surface can be increased by supplying water from sprays or wallows, but this is limited to the saturation pressure corresponding to the skin temperature. Maximum surface evaporation can probably be accomplished with a combination of sprays, or wallows, and increased air flow. Kelly *et al.*[11] provided sprays and showers for beef cattle. Eight Herefords that had access to a shower operated by an electric eye gained an average of 0.37 pound more daily during a 66-day feeding period than the control group. An average gain increase of 0.22 pounds per day was obtained the following year in a similar test during an 80-day feeding trial. In two tests where fogging nozzles were used to spray cattle, there were no beneficial effects from the foggers—in fact, the daily gain of the fogged group was slightly less than that of the control group. The foggers may have actually decreased the evaporation potential by increasing the vapor pressure of the air. Wallows, of course, are generally beneficial for hogs.

Animal surface evaporation could also be increased by reducing the vapor pressure of the air but this would involve reducing the moisture content of the air and would not generally be practical.

Conduction

The relationship representing conduction heat transfer is:

$$q_k = UA\ (t_{ab} - t_s)$$

The rate of heat transferred by conduction is dependent primarily on a temperature difference between two boundaries of a system. In considering conduction heat loss from animals it is convenient to consider the body as a complete system so that the boundary temperatures are the internal body temperature (t_{ab}) and the surface temperature (t_s). Then U is the over-all coefficient of heat transmission of the animal body and A is the body area. Internal body conduction is of great importance because it is the primary means by which heat moves from the internal body to the surface so that it can be lost by some other means.

On the other hand, conduction as a means of external heat loss is relatively unimportant. About the only means of increasing the external conduction is to reduce the animal surface temperature (t_s) by contact with a cooler surface. The area (A) is then only the contacting area. This has been done with swine by providing cooled slabs of some kind and can be a practical aid because they spend so much time lying down during hot weather. In Imperial Valley tests, pigs with access to a concrete slab with a surface cooled to 70°F. gained about 0.25 pounds more per day during a 70-day feeding period than a control group that had access to a wallow. They used 66 pounds less feed per 100 pounds of gain.

Cooled Drinking Water

Although it is probably not an external heat loss factor, cooled drinking water was supplied to beef cattle in tests in the Imperial Valley[11]. In five years of tests the daily weight gains of beef cattle were repeatedly increased by cooling their drinking water from 90 to 65°F. These increases were as high as 0.5 lb. per animal. In most areas the supply water temperature would not be as high as in the Imperial Valley so the cooling problem might, instead, be a problem of proper storage and distribution to insure that the cattle receive it at low temperature.

Air Temperature

Air temperature is a factor common to all four methods of heat transfer, either directly or indirectly, because of the relationship between air temperature and animal surface temperature. Heitman *et al.*[5] found that optimum constant temperatures for swine in a controlled temperature chamber varied from 75°F. for 100-pound hogs to 64°F. for 350-pound hogs. Others have established similar optimum temperatures for other classes of livestock. It is almost certain that some increase in production will be obtained during hot weather if the air is cooled but, because of cost, air conditioning has not been generally established as an economically feasible step in hot-weather production of livestock. For this reason the authors feel that the more practical possibilities should be exhausted first—for air conditioning can always be used at such a time as it becomes an economic expedient.

Summary of Recommendations

The following list summarizes the recommendations proposed by the authors, based on a rationalization of the four fundamental equations of heat transfer presented, and substantiated by field and laboratory tests. These are limited to recommendations the authors consider to be of practical importance in improving the environment for livestock in high temperature areas. It should be kept in mind that the benefits from these recommendations are not necessarily additive.

A. For all classes of livestock
   1. Shades
      a. High or louvered to utilize cool sky.
      b. Long and narrow — oriented east and west.
      c. Use materials with radiation characteristics of white paint on top and black characteristics underneath—use hay where suitable.
      d. Slope slanted shades with high side north.
   2. Use wire-fence pens—if board, use wide spacing.
   3. Keep buildings and warm, or sun-heated, objects away from animal pens and corrals.
   4. Keep area surrounding pens and corrals in alfalfa or some grass where possible.
   5. Lower temperature of surroundings with trees and additional shades, but do not block air flow.
   6. Locate animals in unobstructed wind path or on a hill.
   7. Paint animal buildings white.
   8. Keep animal drinking water cool—small shade over shallow trough.
   9. Feed near or under shade.
   10. Water near but *not* under shade.

B. Beef Cattle
   1. 60 ft^2. of shade per animal.
   2. Showers that adequately wet animal surface.
   3. Fans where air movement is low.

C. Swine
   1. 15 ft^2. of shade per animal.
   2. Wallows.
   3. Concrete floor, or a slab, cooled with surface moisture.
   4. Combination of air movement with wallows or sprays.

Finally, it should be emphasized that the results thus far obtained illustrate several ways of obtaining more uniform environmental conditions under which to conduct genetic experiments with livestock, or of ensuring reasonably uniform but contrasting sets of conditions under which to study the physiological reactions or measure the genetic ability of animals to withstand environmental stresses.

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BREEDING CONSIDERATIONS IN RELATION TO CLIMATIC PROBLEMS

ROBERT R. SHRODE*

ALTHOUGH the word "heat" was prominent in the announced title of the Little Rock symposium, my own experience and, undoubtedly, that of other workers indicates that we are confronted with "climate" in all its numerous interacting aspects rather than with extreme heat alone. This broader approach was reflected in the discussions at Little Rock. The fact that extreme heat is the most noticeable characteristic of the climates in which we have been working has been responsible for the prominence of "heat" in the thinking and terminology in this particular area of livestock research. The variety of concepts of what constitutes "heat tolerance" in an animal typifies the differences of opinion existing on many points in this general problem area. A physiologist generally focuses his attention on the animal's heat regulatory ability and, thus, may define "heat tolerance" as the ability of an animal to approach maintaining a constant body temperature under heat stress. An animal husbandman, on the other hand, who is supposed to be a physiologist, a nutritionist, a geneticist and an economist, may say that "heat tolerance" is the ability of an animal to continue satisfactory economic performance under heat stress. My own thinking has evolved to the point that I am inclined to prefer the animal husbandman's definition but with more emphasis on climate in general rather than extreme heat alone since heat is only one of the many aspects of the climates with which we are concerned.

As evidenced by other papers in this series, a great deal of research with physiological emphasis has been conducted, and the results have been published. In contrast, very few papers have appeared to throw much new light on the genetic aspects of the problem of improving animal production in climates generally referred to as "hot" climates. Since the estimation of heritability has become such a prevalent pastime for animal husbandry research workers, it seems that we could have expected at least a "rash" of estimates of heritability of the many variables the physiologists measure in their "heat tolerance" research. However, relatively few such estimates have been published. I am certain that this does not mean that many heritability estimates have not been calculated. I do not know, but I suspect that others have had the same experience as I have had in estimating the heritability of such things as daily range in rectal temperature, respiratory rate, etc. The lack of consistency of results has been so striking that publication would contribute more confusion than clarification. The variables generally measured in "heat tolerance" studies are correlated with so many other variables such as age, stage of gestation, stage of lactation, and level of production that the amount of adjustment indicated is discouraging, if not prohibitive, if one is to obtain reliable estimates of heritability.

Climatic Adaptability

Ever since the commendable pioneering efforts of Bonsma[1, 2, 3] and Rhoad[4, 5, 6], it has been obvious that genetic differences are, at least in part, responsible for the observed differences in animal response to climatic stress. Such genetic differences have been undeniable in view of the striking breed differences which have been observed. As everyone knows, crossbreeding was undertaken with considerable success in the case of beef cattle, wherein cattle of European origin were crossed with cattle of several of the breeds of India. Most of this crossbreeding was of a continuous nature for producing crossbred commercial beef animals for slaughter purposes. However, it is common knowledge that some of the crossbreeding was directed toward the development of new breeds. No one can deny that the

*Professor of Genetics, A & M College of Texas, College Station.

introduction of the Indian breeds into beef cattle breeding in the South has met with great success. No such striking success has been enjoyed by those who have employed the same procedure in the breeding of dairy cattle. The failure of the dairy cattle breeders to, as yet, parallel the experience in beef cattle breeding is, no doubt, due to several circumstances, known and unknown. Primary among the known reasons for the slowness with which the dairy cattle crossbreeding has moved is the smallness of the numbers of animals employed in the projects undertaking the crossbreeding. Accumulating evidence of the extent to which climatic adaptability varies within our pure breeds is leading many people, who once thought otherwise, to believe that crossbreeding with Indian cattle is not the only breeding procedure that can effectively improve beef and dairy production in many parts of the South. The continued existence of purebred cattle of the European breeds throughout the South indicates that selection within these pure breeds has always been considered by some persistent breeders as an effective method of improvement. The selection emphases may have been misdirected, but natural selection for climatic adaptability has been operating, at least to a certain extent, and the animals have survived and reproduced without year-round air conditioning.

In such a discussion as this I am reluctant to make definite statements because they are seldom justified. My ten years' experience in attempting to learn something about "heat tolerance" in farm animals has served primarily to reduce my store of definite convictions. I once believed that we might soon learn enough to measure and select for "heat tolerance" or "climatic adaptability" directly and, by improving this trait, enhance the ability of animals to perform economically. Although progress has not been as rapid as I had hoped for, research in this area should be continued as well as in the development of managerial ways to improve animal production. However, our present effort as breeders can best be directed toward development and use of the most effective methods of selection based on objective measures of performance with respect to economic traits.

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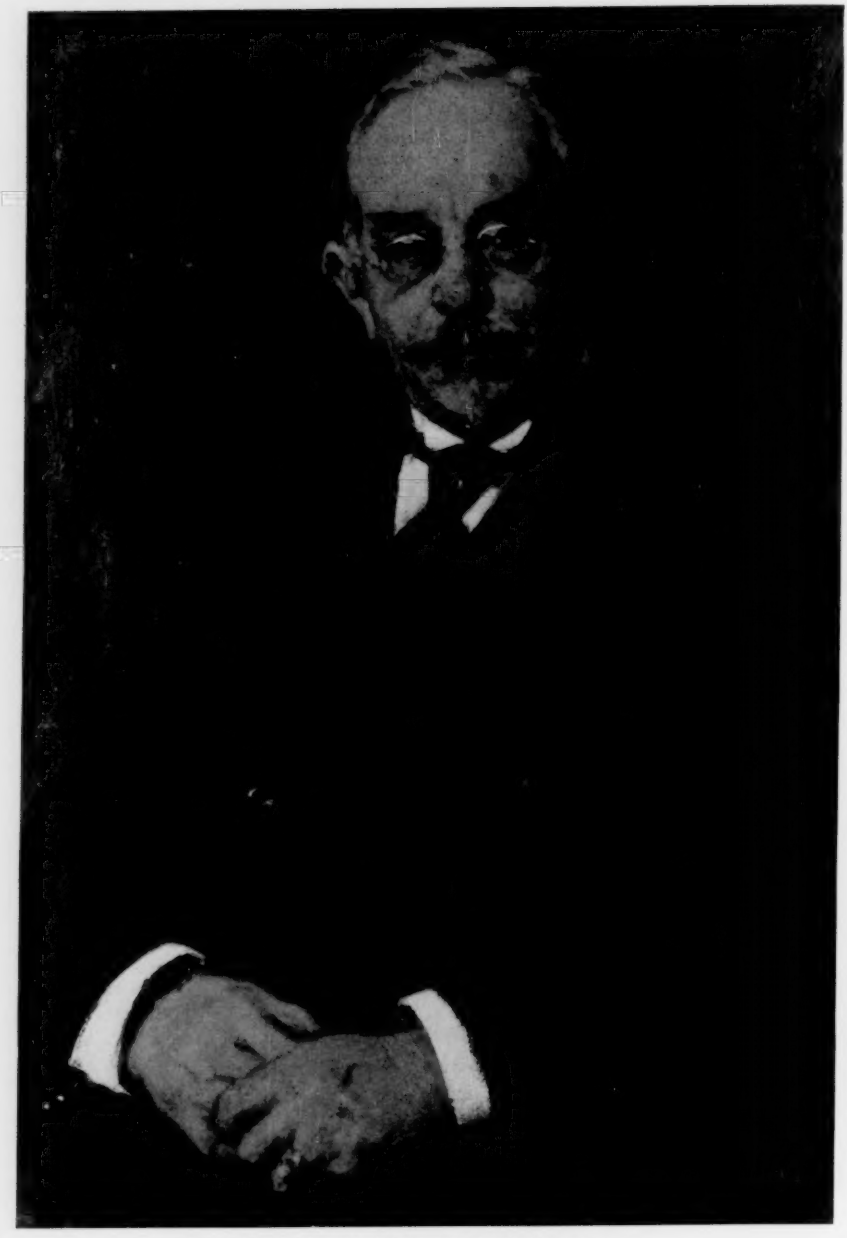


WILHELM LUDWIG JOHANNSEN

1857-1927

WILHELM JOHANNSEN

The Creator of the Terms Gene, Genotype, Phenotype and Pure Line

ØJVIND WINGE*

IT was a man endowed with remarkable intelligence and an unusually critical insight into biological phenomena who first saw the light of day in Copenhagen one hundred years ago this year on the third of February.

Wilhelm Johannsen was the son of a Danish army officer who participated in both of the Schleswig wars, 1848 and 1864, and who was characterized by a great fondness for order and punctuality. His mother cherished a strong interest in both plants and animals, and Johannsen himself was of the opinion that his father's sense for concrete objects as well as fine nuances combined with his mother's appreciation of nature was the inheritance which was responsible for his becoming a scientist.

From his sixth to eleventh year the boy was sent to one of the best schools in Copenhagen, but in 1868 his father was transferred to the town of Helsingoer, which is separated from the coast of Sweden by a four kilometer-wide sound, called in Danish the Oeresund. In past centuries Helsingoer was of much greater signfiicance than it is today, for the southern part of Sweden once belonged to Denmark, and the town with its fortress, Kronborg, was able to control all navigation headed for Copenhagen and the countries lying on the shores of the Baltic: in Helsingoer a heavy duty, the "Sound Dues", was exacted from all foreign vessels. The Sound Dues, which were finally abolished in 1857, actually amounted to two-thirds of the total income of the State. Even in Johannsen's childhood, Helsingoer still bore the imprint of its former greatness. Residing foreign consulates gave it a cosmopolitan atmosphere and provided practical experience in learning foreign tongues. At an early age Johannsen was well versed in languages, particularly German, which his maternal grandmother, who lived with Johannsen's parents, spoke daily.

At the age of 15 Johannsen passed the so-called "preliminary examination", which meant that he would be entitled to study at the University in Copenhagen. His father's modest army salary and the fact that an older brother was studying to be a civil engineer unfortunately prevented the realization of this plan and, instead, he was placed in an apothecary's shop for the purpose of becoming a pharmacist. Here he had the opportunity of carrying out some chemical experiments on his own, and in this he was aided by his elder brother. Some years later Johannsen is found working in an apothecary's shop in the German-speaking part of Denmark called Angel; it was in this part of Denmark that he first turned, with enthusiasm, to the identification of plants and to the study of plant physiology, and it was not long before he had passed a German pharmaceutical examination in Kiel. A minor eye disease caused him to interrupt his studies of pharmacy for a year, which time he spent as a pharmacist's assistant in Sachsen in Germany. Here he had the opportunity to make use of a large library, undertake mountain excursions, and identify plants. The German language he now mastered completely.

Johannsen returned to Denmark in 1879, 22 years of age, and during the next year he completed his pharmaceutical examination with high honors. With the help of a stipendium and a small inheritance he was able to continue his studies, especially botany and analytical chemistry, for yet another semester. One of his teachers of botany in Copenhagen was the well-known botanist, Eugenius

*Carlsberg Laboratorium, Copenhagen, Denmark. This lecture was delivered November 5, 1957 at the University of California, Berkeley.

Warming, whose lectures I, too, have had the pleasure of attending, although at a much later period.

After working in the Danish provincial town of Aalborg with a pharmacist who appreciated Johannsen's scientific interests and who equipped a small analytical laboratory for him, he was appointed in 1881, through the support of Professor Warming, as assistant in the Chemical Department of the newly founded Carlsberg Laboratorium in Copenhagen.

The head of the Chemical Department at this time was the brilliant Johan Kjeldahl, whose name is internationally known in connection with his method for the determination of nitrogen in organic substances.

Johannsen had now really set forth on his scientific career, but it should be kept in mind that at this time he was a pharmacist and had not even a University degree.

At the Carlsberg Laboratorium he was given a free hand. The laboratory had been founded by a wealthy and farsighted brewer, J. C. Jacobsen. The Carlsberg Foundation, which still plays an important role in the life of Denmark, was also established by Jacobsen. According to the statutes of the Foundation, the profits derived from the Carlsberg Breweries, which it owns, are to be used exclusively for the promotion of science and art.

Among other things at the Carlsberg Laboratorium Johannsen studied the anatomy of barley and wheat grains. He remained at the laboratory for six years, during which time he made several journeys to other lands. A short time was spent in Tübingen with Professor Pfeffer, and he was also in Paris, Darmstadt, Zürich, and Vienna. In 1887 he resigned his post at the Carlsberg Laboratorium but nevertheless continued some of his studies there during the years 1890-94. It was at Carlsberg that Johannsen first began his work on variability in barley and on dormancy in plants.

Johannsen was a great reader, and he related that one of the books which interested him most at this time was Claude Bernard's classic, "Leçons sur les phénomenes de la vie communs aux animaux et aux végétaux". A craving for intellectual stimulation in other fields led to the study of history and medicine and of psychology, and he considered Höffding's "Psykologi" (1892) to have had much influence on his way of thinking.

In 1892, at the age of 35, Johannsen was appointed lecturer in botany and plant physiology at the Royal Veterinary and Agricultural College in Copenhagen.

I do not think that many are aware that it was Johannsen who first developed a method for waking plants out of their normal winter dormancy; this was accomplished by etherization. On the basis of this work, Professor Warming in November 1893 at a meeting of the Royal Danish Academy of Sciences demonstrated branches of willow in leaf and sprouting potatoes, just as though the winter had been transformed into spring. Johannsen subsequently improved his method so that it could have practical interest for gardeners. This discovery caused quite a sensation and before long the method was employed not only in Denmark but in other countries as well. At the present time the winter dormancy of plants, especially lilac, is often arrested by treatment with hot water, but the type of treatment is of minor importance. It is characteristic of Johannsen that his publications on theoretically important discoveries often appeared in Danish horticultural or agricultural journals so that considerable time would elapse before they were known to the scientific world at large. However, with regard to his work on dormancy, Johannsen did submit a lengthy paper (unfortunately only in Danish) to the *Journal of the Academy of Sciences* entitled "On antagonistic activity in metabolism, especially during maturation and dormancy," and in Germany he published a book entitled "Das Aether-Verfahren", which enjoyed two impressions, the second in 1906. In 1898, the year after the publication of his paper in the *Journal of the Academy of Sciences*, he was elected to membership in the academy.

Gradually Johannsen's chief interest was centered around the problem of variation in self-fertilized plants, especially barley (*Hordeum vulgare*) and Princess bean (*Phaseolus vulgaris*). He undertook isolations of the progeny of each plant through many generations according to the principle of the Frenchman, Vilmorin, and he studied in detail the effect of selection. Standard statistical methods were employed, and in this his elder brother, who had studied mathematics, was of much help to Johannsen.

From 1893 to 1897 Johannsen carried out

these individual progeny analyses in barley, using variability statistics and calculations of correlative variability with respect to weight and nitrogen content of the grain. He found that although there was a correlation between high weight and high nitrogen content, it was by no means inviolable, and that no difficulty was encountered in producing a large-grained race with a nitrogen content so low that it could be regarded as a good malting barley.

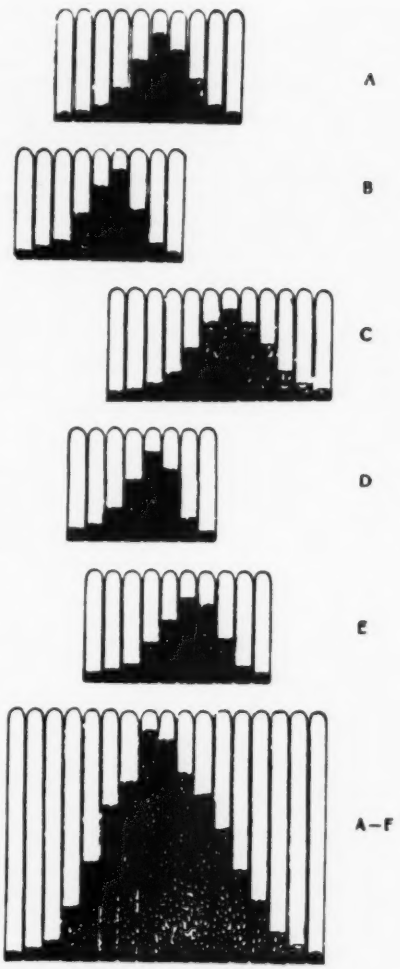
By 1902 Johannsen had not yet any clear conception of phenotypic and genotypic variation. He speaks at this time of "individual variation" as something inherent in the organism itself and bearing no relation to the environment. He speaks, too, of individuals fluctuating around a main type, even when the effect of the environment is negligible.

In 1903 Johannsen created the expression "pure line", and in the same year his classical work appeared, "On Inheritance in Populations and in Pure Lines", in which he formulated a new interpretation of Galton's law of regression. Regression is total in pure lines, but in mixtures of pure lines one will find Galton's partial regression, a phenomenon which is theoretically expected to occur on the basis of a simple calculation of probabilities. Partial regression is a statistical term for the fact that a given phenotype most probably belongs to the biotype which it most closely resembles.

This can be illustrated by Johannsen's diagram (Figure 8) of the results of his studies on Princess bean (*Phaseolus*). From a given population a number of pure lines can be isolated which differ in respect to the size of the seed. Since bean plants are self-fertilized, each line, in the absence of mutation, will be homozygous (a term created by Bateson in 1902) and therefore the variation in seed size found within a single line and within the single plant will be purely phenotypic, and selection within such a line will be without effect. The picture is, of course, entirely different when a number of pure lines are mixed together.

The year 1903 is in many respects a fateful one in the history of genetics. At the same time that Johannsen made his most important contribution, he became aware of the rediscovery of Mendelian segregation by de Vries, Correns, and Tschermak. There is no doubt that the demonstration of the constancy of the factors of inheritance, the genes, was decisive for Johannsen's conception of absolute constancy of pure lines.

The long-established and deep-rooted convictions of biology were, however, difficult to eradicate, and when Johannsen in 1907 presented a lecture before the Royal Horticultural Society in London with the title, "Does Hybridization Increase Fluctuating Variability?", his ideas were received only half-heartedly by the geneticists who attended the meeting. Plate from Berlin, Yule from London, and partly Bateson himself, who acted as President on this occasion, expressed themselves in words to this effect in the discussion which followed the lecture. As the years passed, however, the truth of Johannsen's claims was generally recognized, including his assertion that Galton's law of regression was based on false conceptions and impure material. It is difficult to overestimate the significance of



JOHANNSEN'S DIAGRAM

Figure 8

Johannsen's diagram shows the results of his studies on the Princess bean. From a given population a number of pure lines were isolated which differ in regard to size of seed.

Johannsen's work for the correct evaluation of both Darwinism and Lamarckism.

In 1905 Johannsen was appointed *professor ordinarius* in plant physiology at the University of Copenhagen. This event occasioned some reaction in the press, for it was felt by some that a man without any University education was not qualified to become a university professor, but such scruples were forgotten with Johannsen's ever-increasing renown. In 1910 he was named *doctor honoris causa* in medicine and in 1917 became rector of the University. During the course of years many academic honors were awarded him outside of Denmark.

It can perhaps be said that after his elucidation of the concept of pure lines and all that it entails, Johannsen's contributions were no longer in the field of experimental science. He had enough to do in studying and interpreting the consequences of his discovery. The last 20 to 25 years of his life were spent in the fruitful capacity of both author and critic, his esteem and renown increasing with the years. He was endowed with the ability to erect many-sided views of a given phenomenon and to come forth with explanatory arguments and illustrations which very few others would even have thought of. He was at all times lively and discerning, sometimes a bit sharp, and sometimes even rude in his criticism.

In the year 1909 Johannsen's greatest work, "Elemente der exakten Erblichkeitslehre", appeared and brought him fame both as a biologically-trained statistician and as a critic. It was in this book that he first proposed the use of the word "gene" and introduced the concepts of genotype and phenotype. On the occasion of Johannsen's seventieth birthday the renowned Finnish geneticist, Federley, wrote of this book in the following words: "One must be a writer by the grace of God to be able to endow a book like "Elemente" with such magic power as it today, in its third edition, still retains. Its author combines Gallic spirit and clarity with German temperament and Anglosaxon objectivity, and conciseness with Danish wit—all of which results in style which is uncommonly rare among scientific authors." The third edition appeared in 1926, and it was a pleasure to note that Johannsen, now in his 70th year, was able to keep abreast of times and to recognize the significance of some of the newest results in genetics and also in cytology, a field which he had long viewed with some distrust. He first became reconciled to the chromosome theory at an advanced age and this was undoubtedly due to the fact that he himself had never worked with chromosome cytology.

I remember one autumn day in 1911 in the Botanical Garden in Copenhagen where I happened to meet Johannsen, who was at that time preparing for his departure for the United States where he was to hold a series of lectures at American universities. That day he expressed a strong doubt that cytology, (especially with respect to chromosomes), would ever have any interest for genetics. "Man has 10 fingers, 32 teeth, and so and so many chromosomes. One is a character just as much as the other"—these were his words. The concept of heritable factors as tangibile, localized units was at that time irreconcilable with his views; it was almost as though such an explanation were too coarse for his tastes. For the same reason he often criticised the use of the word "gene" to denote something completely material and tangible—"this only compromised the word", he said.

In his publication in the University's *Festskrift* for 1914 entitled "False Analogies", he considers the problem which was now constantly in his mind—that of chromosomes and genes. Thomas Hunt Morgan's epoch-making investigations on *Drosophila* clearly pointed to the dominant role played by the chromosomes as the bearers of the genes. First in 1896 and on several other occasions Johannsen had criticised Weismann's theory of the germplasm ("Determinant-Lehre"), according to which the cell nucleus was supposed to contain a definite hereditary particle for each organ. Johannsen was certainly justified in his criticism of this theory, but at the same time he would not accept the idea that variation in the progeny of a hybrid could be due to a reduction division preceding the formation of the sexual cells. In 1896, before Mendel's segregations were rediscovered, he had written concerning the germ plasm theory the following: "When such an extremely simple explanation of enigmatic biological processes captures the fancy, especially when it is propounded with the flowing eloquence and dexterous dialectic of a Weismann, we dare not pass over the subject in silence," and thereafter he begins his arguments against it. Again, in "False Analogies" he writes: ". . . and Weismann still assumes that the 'stirps' lie in the filamentous structure of the cell nucleus (those structures which are called chromosomes). This is nothing but pure speculation, but, at the same time, it is an idea which found support in certain facts and which does not seem unreasonable as a working hypothesis for the present." And he adds as a footnote, "The present author does not accept the correctness of this hypothesis." That was in 1914!

In the third edition of Johannsen's book, "The Historical and Experimental Aspects of Inheritance", which was written in Danish in 1918, he did, however, acknowledge the importance of cytology, and this view was repeated in his later works. At his death in 1927 I believe that he was truly convinced that the chromosomes were the bearers of the genes; he, at least, did not protest against the use of the word "gene" to designate something concrete in the form of a localized factor of inheritance.

It might be well to mention that other

geneticists of this period also found it difficult to reconcile their views with Morgan's theory of the chromosome. For example, the well-known German geneticist, Edwin Baur, long insisted that genetic analysis of hybrids only involved "differences" between the parents, and that cases of what we now call triple allelomorphism were "some most singular and aberrant 'Dreieck-Falle'." Baur did not originally conceive of these differences as arising from concrete elements in the chromosome, although he later accepted the gene theory.

On the other hand, it is quite correct that geneticists can only study differences. Even with the enormous interest shown by present-day geneticists in biochemical mutants, it is safe to say that detailed biochemical knowledge is scanty. It can therefore be of interest to devote some words to Johannsen's conception of the innermost nature of the organism.

For him it was a striking fact that most of Morgan's *Drosophila* mutants were concerned with inherited and analyzable characters which expressed themselves as direct abnormalities—for example, winglessness, eyelessness, lack of eye pigment, abnormal leg structure, etc. The inheritance of a character, the presence or absence of which could separate two species, was not investigated in Morgan's experiments. Johannsen pointed with justification to the fact that even such a strongly defective fruit fly as one of these mutants would always remain a *Drosophila melanogaster* and would never be considered to be another species. Following this line of argument, he asked whether it was not possible that only the superficial and unessential characters were due to inheritable factors localized in the chromosomes, while the essential characterization of the species was determined by other cellular components, in particular the cytoplasm? If such is the case, then specific characters are not genetically analyzable, and the most significant part of the experiment is thus relegated to the non-analyzable portion of the crossing.

These thoughts of Johannsen certainly constitute an important problem which has not yet been solved. Although it is true that there has gradually accumulated evidence for the occurrence in fertile hybrids of segregating specific characters, Johannsen's emphasis on the often inferior and superficial nature of genetically analyzed characters is worthy of speculation.

Johannsen described his own life as being somewhat incredible. The fact that he was prevented from studying at the University he originally considered to be a great misfortune, but in later life he changed his views. His attainment of a first-rank position as a scientist was by irregular means; the fact that he, for the most part, was self-taught probably caused him to look at problems in a special way—unrestricted by authority yet in full harmony with his intrinsic originality. With regard to genetics, he himself felt that his successes in this field were mostly due to his emphasis upon physiology, rather than upon the more traditional morphology which was employed by botanists and zoologists, and he experienced several times a complete lack of understanding of his genetic investigations among naturalists of the old school. We find, for example, in one of his surviving memoranda the following words: "That training which, even in my youth, our naturalists received has, partly due to its almost purely descriptive direction, provided them with blinkers which I, with all my scientific unsophistication, thank Heaven for that I lack, even though my glance is thereby more scattered, more shifting, and often too little concentrated in one direction—I am, and always will be, a free-lance in science."

From his early youth Johannsen was possessed with an insatiable craving for knowledge, for comprehension and understanding, and for enrichment of his mind and spirit. He read voraciously, but by no means limited himself to that field of science in which he actively participated nor even to related fields, but cast himself with enthusiasm into all realms of science as well as philosophy and esthetics. He had a remarkable ability to assimilate and retain the significant parts of his reading, and in the preparation of his manuscripts he was able to depend to a high degree upon his memory. Subjects which interested him particularly, aside from science and philosophy, were history—especially, the history of England—biography, and Danish and German literature; he was particularly well-versed in Goethe and Heine.

As a scientist Johannsen was characterized by his vigorous fantasy which acted in pleasing harmony with his clear thought and his sharp critical sense. In all of his investigations he constantly strove to be as exact as possible and to express as much as possible in terms of figures, measurements, and weights. He was an uncompromising opponent of all scientific research which did not employ accurate methods; it is partly for this reason that he came to hold a rather poor opinion of ecology, a field which during the nineties had made noteworthy strides. This led to an unfortunate impairment of the relations between Johannsen and his highly admired teacher, Eugenius Warming. Professor Warming was a declared Lamarckist and believed in the environment's direct heritable influence upon the organism. It was thus unavoidable that he often became the object of Johannsen's harsh criticism, but it must be admitted that Warming's understanding of the scope of Johannsen's contributions to genetics was rather limited.

As a lecturer, Johannsen was absorbing and fascinating. His excellent memory and distinguished learning, his wealth of ideas, his clarity, and the ease with which he could express himself—all contributed to elegant treat-

ments of the most difficult subjects, which were thus made easily accessible to the listener through the brilliance of their execution. His lectures were always full of life and wit, often spiced with appropriate citations, but at the same time outstanding in their clarity of thought, and in this remarkable combination of lightness, humor, and stringency lies the secret of their excellence.

His linguistic proficiency was to him a good help in the writing of his numerous books and papers. His well-known "Elemente der exakten Erblickheitslehre" was written in faultless German, and as President for the International Seed Control Congress in Cambridge in 1924, he was able immediately following each lecture, to abstract it verbally into the two other main languages of the Congress.

Johannsen had from nature's hand a joyful and lively temperament. It is told that in his childhood one heard him singing as soon as he awakened each morning, and this happy nature he retained throughout his life and it marked his association with others. He invariably had something cheerful to say upon meeting and seemed to spread joy and well-being about him.

Johannsen found deep happiness in his marriage. Both he and his wife were exceptionally fond of entertaining their friends, and their home was always a pleasure to enter, characterized as it was by culture and hospitality. On many occasions, particularly in his old age, he was able to hold the whole party entranced by his brilliant wit.

As already mentioned, Johannsen, after having demonstrated the heritable constancy of pure lines, did not further pursue experimental science. "I'm resting on my laurels," he said one day to me, not without a touch of sarcasm. The people of many nations visited him throughout the years to be able to see the master himself and the classical pure lines of *Phascolus*. I remember that on the occasion of such a visit he telephoned to me and said, "A Dr. N. N. from Cornell University is here. I have shown him A) myself and B) my beans. Will you receive him now?"

This humorous tone, so characteristic of Johannsen, and implying the *da capo* nature of such visits, is indicative of the extraordinary esteem in which he was held by his contemporaries. They wanted to see him "with their own eyes."

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